Patterns of predator-prey dynamics between gray whales (*Eschrichtius robustus*) and mysid species in Clayoquot Sound

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ABSTRACT

The patterns of foraging intensity of gray whales (*Eschrichtius robustus*) over a 17-year period (1997–2013) in Clayoquot Sound, Vancouver Island are examined. In this area, epibenthic mysid species are gray whales' primary prey. The analysis indicates a top-down modification on habitat quality by this apex predator. Intense foraging in one or two summer season contributes to reduced prey resources available in the following summer. Years of heavy predation pressure were followed by at least one year of reduced foraging, probably allowing a reprieve in which the mysids could repopulate. Over the time span several patterns were noted including: boom-bust cycles; extended periods of reduced foraging; an overall declining trend of foraging whales using Clayoquot Sound, followed by a significant prey recovery in 2010. Life history patterns of mysids are discussed in the context of their ability to recover from predation, and how this recovery during a reprieve may buffer the intensity of foraging from the previous year. The continuing ability of mysids to recover from repeated and persistent removal will determine the use of Clayoquot Sound as a gray whale foraging area in the future.

KEYWORDS: PREDATION; FOOD/PREY; FEEDING GROUNDS; PACIFIC OCEAN; SURVEY-VESSEL; TRENDS; NORTHERN HEMISPHERE

INTRODUCTION

Predation shapes community structure by exerting top-down pressure. When positioned at the apex of an interaction web, cetaceans are both consumers, and in some cases habitat architects (Highsmith *et al.*, 2006; Oliver and Slattery, 1985). Whale distribution is, however, determined by prey location and abundance, which in turn, is under the influence of bottom-up forces of plankton blooms or benthic primary production. Therefore, the life history of both the predatory whales and their zooplankton prey shape the strength of their interaction, consequently creating the spatial dynamics of whale populations and foraging patterns over time.

Temporal patterns of use by gray whales (*Eschrichtius robustus*, Lilljeborg, 1861) of a foraging site in Clayoquot Sound (49°14'36"N, 126°6'10"W and 49°18'51"N, 126°14'30"W) on the west coast of Vancouver Island, British Columbia, Canada were examined (see Fig. 1). Whales have been noted in the area for over 40 years (Hatler and Darling, 1974). Almost 200 individual whales have foraged in Clayoquot Sound since 1997, with many of these (48.52 %) returning for multiple summers (2–12 years, Whale Lab, unpublished photo-id data, pers. obs.). Deep unproductive waters that are devoid of prey border the study area, creating a spatially discrete site that is separated from other foraging sites by at least 25km. There is no evidence to suggest that population mixing between mysid swarms is hindered within Clayoquot Sound, however comparisons between prey populations in the study area and of those sampled in foraging areas 40km further north found them to be genetically distinct (Short, 2005).

This study focused on gray whale foraging patterns in Clayoquot Sound following a prey switch from benthic to epibenthic resources. Having apparently driven local amphipod (*Peracardia, Amphipoda*) reserves into major decline by about 1997 (Duffus, 1996: Burnham and Duffus,

2016), foraging has since targeted swarming mysid species (*Peracardia, Mysida*; Duffus, 1996; Dunham and Duffus, 2001; 2002). Previous work (Feyrer and Duffus, 2014) has shown strong positive correlation between gray whale feeding behaviour and mysid prey density in Clayoquot Sound.
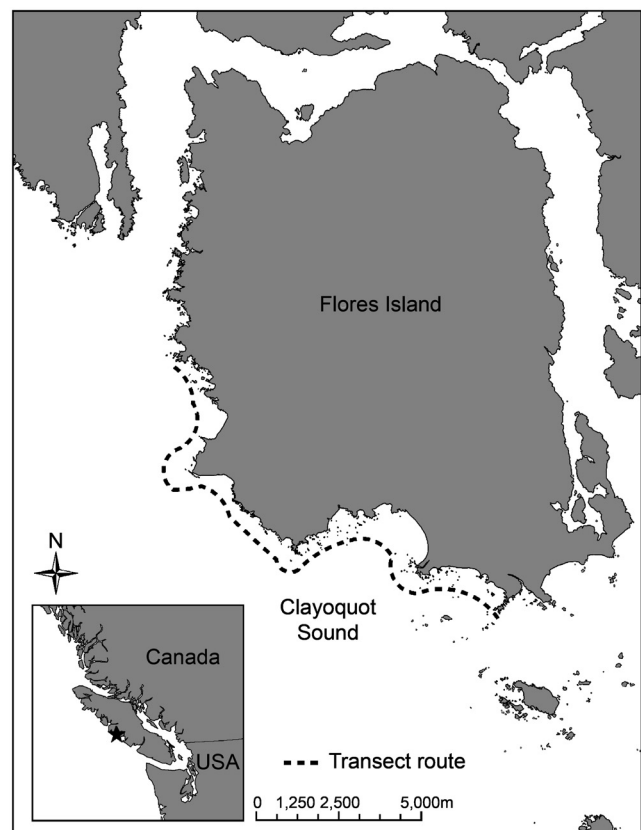

Fig. 1. The study area, Clayoquot Sound. The study area survey route is indicated by the dotted line, approximately following the 10m isobath.

The whale data are considered in light of the patterns of growth and reproduction of mysids. It is expected that cool water temperatures and lower general productivity of the winter months result in lower mysid reproduction. Thus, despite refuge from their major predator over winter, most mysid reproduction is initiated following productivity increases; thus the late summer brood in September becomes a cache/foundation for the following years' prey stock.

METHODS

Approach

The objective of the study was to assess the relationship between gray whale foraging activity and prey abundance over time. The approach taken was to: (1) quantify within-season patterns of whale foraging intensity for each summer in the 17-year span of data collection; and (2) examine whether the magnitude of one seasons' foraging affected the next, in order to determine any between-season patterns in predation. In particular, the number of whales in the late season was compared to those in the early part of the following summer.

The tested hypothesis is that the number of whales foraging in a given year impacts the available prey resources in the next year(s). The expectation is that in years of high foraging intensity (i.e. where prey removal exceeds population growth), prey populations will be depressed the following year. The influence of the number of foraging whales at the end of one season (i.e. in autumn) on the number of individual whales recorded at the beginning of the next foraging season (i.e. summer) was examined on the expectation that heavy autumn foraging would depress mysid reproduction and thus abundance in the following spring, thereby depressing whale foraging effort (whales would move elsewhere) in the subsequent season or seasons.

Field methods

Whale data

Whale data were obtained from boat-based census surveys, each covering approximately 20km² of the nearshore of the long-term study area, on the southwest coast of Flores Island. Although the surveys were conducted predominantly over mysid habitat, the study area also encompassed known locales for amphipods, crab larvae (*Pachycheles* and *Petrolisthes* spp.) and other occasional prey species.

The transect survey followed the 10m isobath (see Fig. 1) and the route, aimed at maximising the possibility of locating foraging whales, was developed by intense observation and surveying between 1994 and 1997. A survey was conducted at least twice a week between 24 May and 8 September for the years 1997 to 2013. Differences in the timing and number of surveys in each season (see Table 1 and Results) were due to weather conditions.

Vessel speed remained constant at 13km h⁻¹ to avoid double counting, with a minimum of four observers constantly scanning 360° for whales. Surveys were aborted if visibility became reduced or if sea state exceeded Beaufort 3.

Only foraging whales were recorded on transect surveys; foraging was determined by observations of behaviour including dive location, length and distance travelled (Malcolm and Duffus, 2000; Feyrer and Duffus, 2014). Prey habitat locations have previously been well defined through sampling, sonar surveys and modelling (Laskin *et al.*, 2010).

Mysid data

To complement the whale data, 12 prey sampling stations were randomly selected within known mysid habitat strata and sampled monthly during the winter and every second week in the summer over a three-year period (2010–12). Samples were taken by towing a 'bongo' style plankton net with two 30cm openings and a 500μm mesh. The net was deployed, allowing it to sink to the rocky substrate, dragged laterally for at least 30 seconds at an average speed of 4kmh⁻¹, and then pulled straight to the surface. This was repeated three times at each of the stations and the samples pooled to make temporal comparisons. Mysids were preserved in 70% ethanol, enumerated, measured (body length rostrum to telson tip), sexed and identified according to Kathman *et al.* (1986). Gravid females were identified by the presence of a brood pouch with young.

Analysis

Within-season patterns of whale foraging were analysed by the skew and kurtosis of the distribution of the 'whale foraging days' recorded from each survey through the summer (Sokal and Rohlf, 2012). In addition to these metrics, the maximum single survey number of foraging animals and its timing were used to identify the temporal peak of prey demand. The peak date acts as the 'centre point' of the distribution of whale foraging effort, with patterns described relative to this seasonal maximum. Skew is the degree of symmetry around this peak date, whereas kurtosis quantifies the degree to which the distribution is peaked or flattened compared to a normal distribution (Sokal and Rohlf, 2012). They are calculated as:

$$skew = \frac{\sum (x - \bar{x})^3}{(n-1)s^3}$$

$$kurtosis = \frac{\sum (x - \bar{x})^4}{(n-1)s^4}$$

where: $\bar{x}$ is the sample mean; N the number of data points, and s the sample standard deviation.

For analysis of inter-annual patterns, the mean number of foraging whales surveyed per year was compared to the mean over the 17-year period. Years were classified as relatively high or low based upon whale numbers and thus foraging pressure based on this 17-year average. A regression analysis was used to establish the dependence of the number of whales supported by the prey stock in the late spring/early summer of each season to that of the latter stages of the previous season. In all cases, whale presence was used as a proxy for mysid stock size. This assertion is supported by mysid density measurements made in 1996 and 1997 with plankton nets, flow meters and four consecutive years of intense quantitative sonar surveying from 2004 to 2008, establishing a high correlation between whales and mysid biomass (Dunham and Duffus, 2001; Feyrer and Duffus, 2014).

RESULTS

The results from the boat surveys are summarised by year in Table 1 and Figure 2. Between 1997 and 2013, 580 surveys were conducted (annual average, 34.1, range 15–59). The mean number of whale foraging days per year ranged from

just under 1 (in 2007 when surveys occurred on 47 days) to as high as 18.3 (in 2013 when surveys occurred on 23 days) whilst the overall mean was just under 7 whales/survey; the peak date for foraging whales being present ranged from 6 June to 26 August (Table 1, Fig. 2). The maximum number of whales seen on a single survey was 38 individuals (2013, Fig. 2).

Comparison of mean numbers of foraging whales
Table 1 shows that on four occasions, years with a mean number of foraging whales that exceeding the global mean over the period, therefore relatively high foraging pressure (1998, 2002, 2004, 2006), were followed by at least one year

with a mean below the global average value. There were two very high years consecutively in 2010 (16.4) and 2011 (11.3) followed by one low year. There were two sets of three consecutive years with low foraging effort. The 1999–2001 set followed high (9.58) foraging in 1998 while the 2007–09 set following a set of descending high-low pairs between 2002 and 2006. The highest foraging effort in the series occurred in 2013 i.e. the final year.

Temporal distribution of foraging within years
For all years, except 2007, 2010 and 2011, the temporal distribution of foraging whales displayed a positive skew i.e. site utilisation was greater before the peak date. This skew

Table 1
Summary of transect survey data 1997–2013.

| Year	Number of surveys	Sighting period	Mean (SD)	Peak date	Skew	Kurtosis
1997	55	29/06–04/09	6.22 (3.13)	19/08	0.209	−0.387
1998	59	06/06–03/09	9.58 (5.32)	08/08	0.888	−0.825
1999	30	03/06–26/08	3.30 (1.66)	04/08	0.543	−0.661
2000	18	02/06–12/08	3.39 (2.38)	12/07	0.489	0.534
2001	46	25/05–12/09	2.37 (1.59)	13/08	0.696	2.13
2002	42	24/05–05/09	10.74 (7.80)	07/07	0.861	−0.153
2003	30	27/05–07/09	5.10 (2.74)	26/07	0.658	−0.901
2004	26	24/05–12/09	10.65 (8.36)	16/07	0.773	−0.632
2005	26	31/05–07/09	2.23 (1.19)	09/07	0.583	−0.549
2006	32	25/05–08/09	7.13 (5.80)	31/07	1.10	−1.209
2007	47	24/05–08/09	0.936 (1.14)	27/06	−0.168	2.78
2008	15	01/06–04/09	3.33 (2.75)	02/08	0.364	0.611
2009	32	27/05–06/09	3.81 (3.60)	05/08	0.677	0.191
2010	30	26/05–09/09	16.4 (6.54)	26/08	−0.0459	−0.848
2011	36	25/05–06/09	11.3 (6.20)	07/08	−0.821	−0.988
2012	33	25/05–02/09	4.73 (3.08)	06/06	0.266	0.916
2013	23	25/05–01/09	18.3 (8.02)	05/08	0.488	1.34
Overall	580	24/05–06/09	6.96 (4.19)	−	−	−
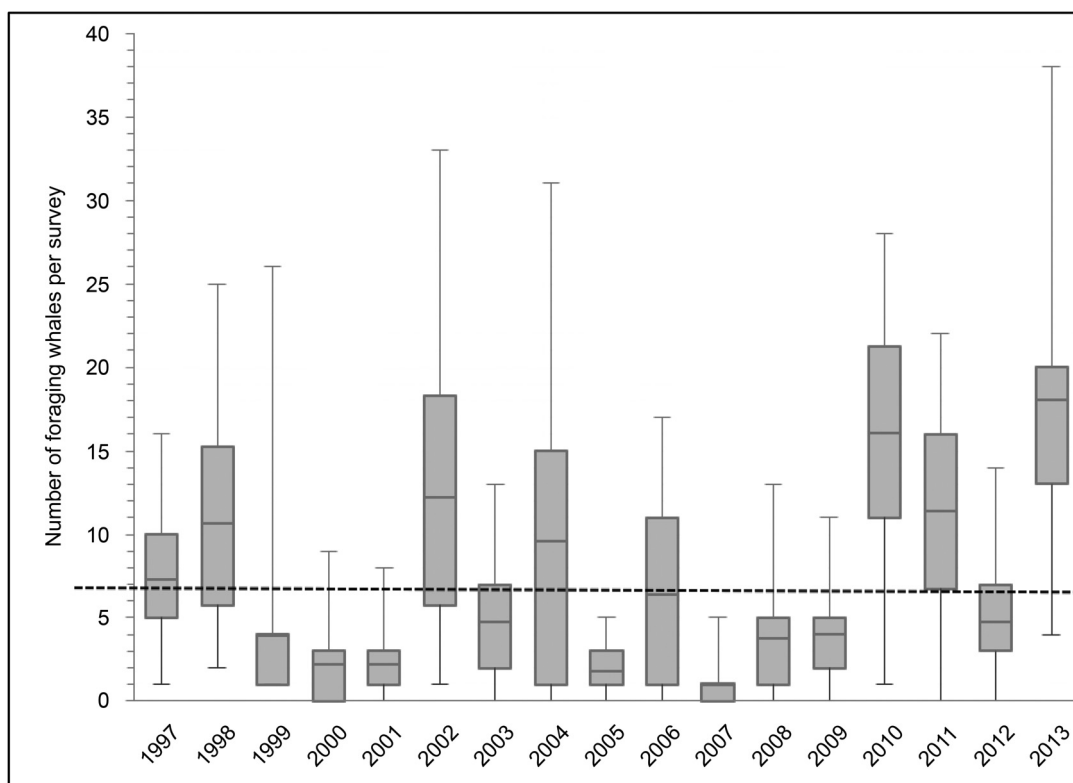
Fig. 2. Boxplot to indicate foraging intensity in the study site, calculated by the number of foraging whales sighted per transect survey. The dashed line is the overall average for all years, and allows for comparison between years.
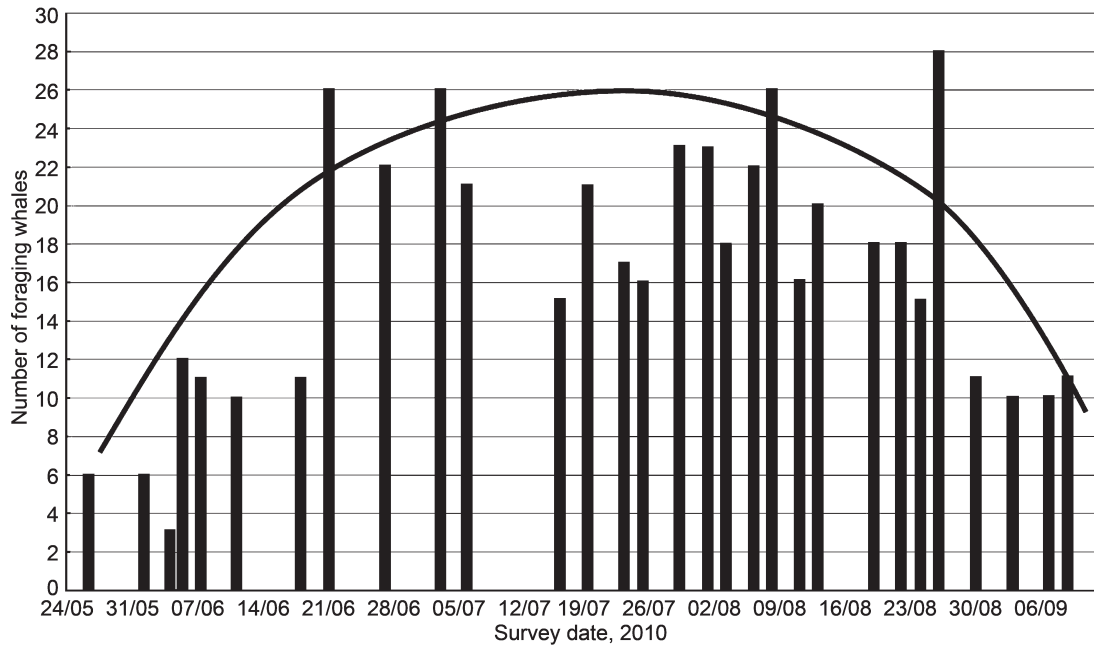
Fig. 3. Survey data of foraging whales from 2010, showing a negative skew and platykurtic distribution. Curve added to highlight skew to the left of the peak date.
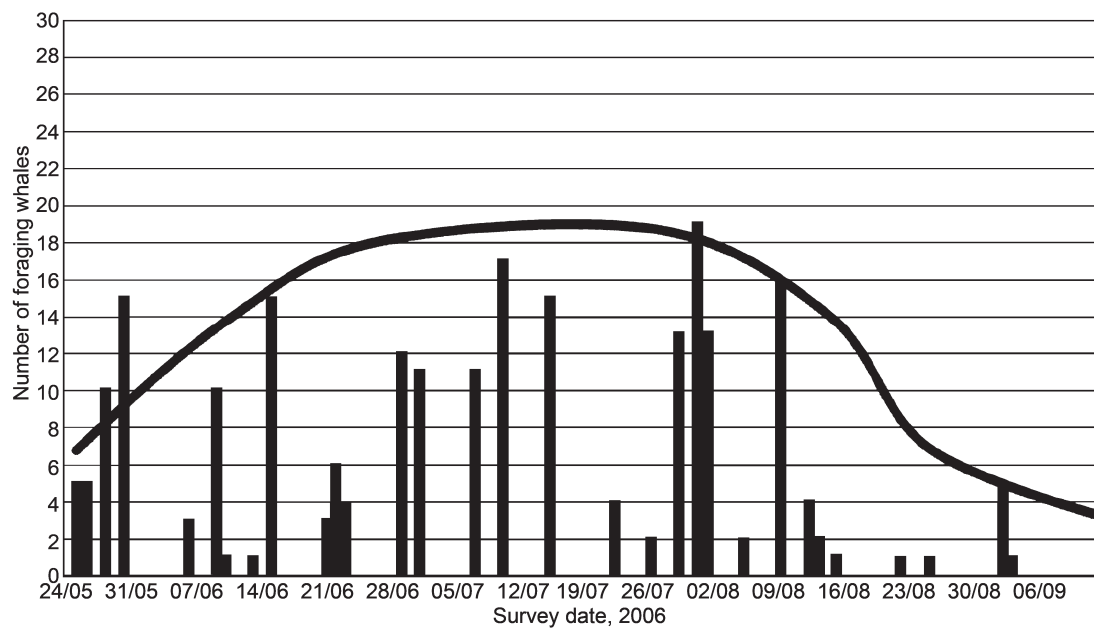

Fig. 4. Survey data of foraging whales from 2006, showing positive skew and platykurtic distribution. Curve added to highlight these features.

was particularly high in 1998, 2002 and 2006 (see Fig. 4) where the presence of foraging whales was predominantly pre-peak and rapidly dropped to almost complete site abandonment in some cases. For the other three years, more foraging whales were observed after the peak date. The relatively early peak date in late June, shaped the negative skew for 2007, despite whale numbers being low throughout the summer (see Fig. 5). For 2010 and 2011, the negative skew (much lower in 2010) was consistent with foraging continuing into the late season, peaking in August for both years (see Fig. 3).

For most (11 out of 17) years, summer distributions were platykurtic (Table 1). The distributions show a flat data spread and more consistent numbers of foraging whales over a longer time span (e.g. see Figs 3 and 4 for 2006 and 2010).

This is contrasted to years where the whale presence is strongly focused around the peak date, e.g. 2009 (see Fig. 6).

Comparison of numbers of foraging whales in subsequent seasons
A regression analysis was performed on the mean number of whales foraging in the last two weeks of the season, (26 August–8 September) and then a similar period at the beginning of the subsequent season (24 May–6 June). The prediction was that intense foraging in the late season would depress early season prey stocks the following year and *vice versa*. The relationship was insignificant ($f = 0.376$, $p = 0.55$, $r^2 = 0.047$) and did not support the hypothetical expectation of dependence. Some of the confounding variables that may obscure such a relationship are discussed below.
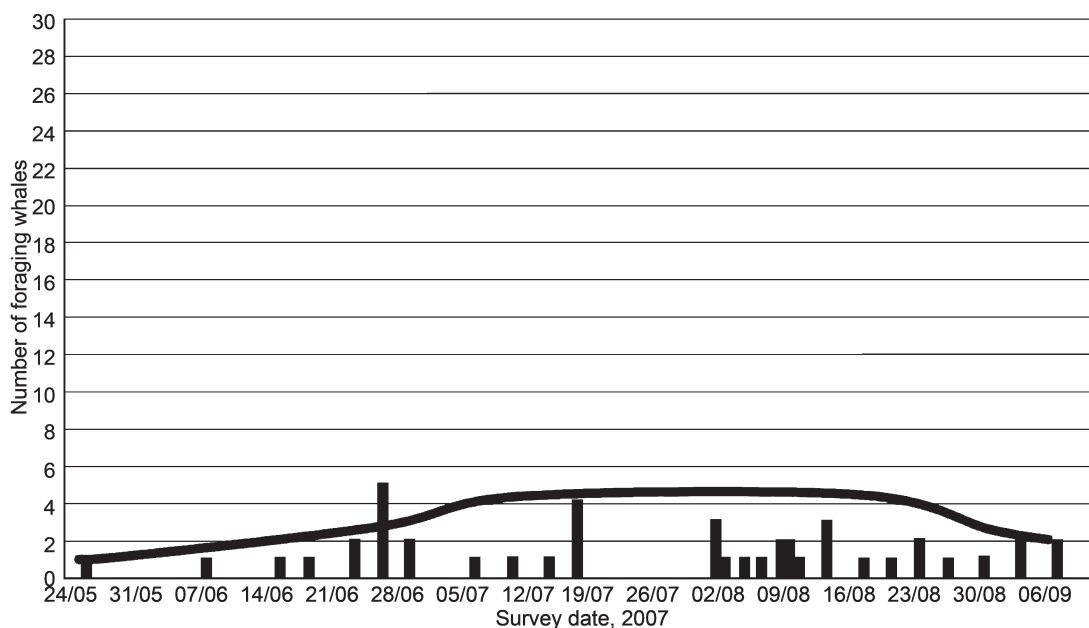
Fig. 5. Survey data of foraging whales from 2007, showing a negative skew and leptokurtic distribution. Curve added to highlight both skew and consistent distribution of whale observations.
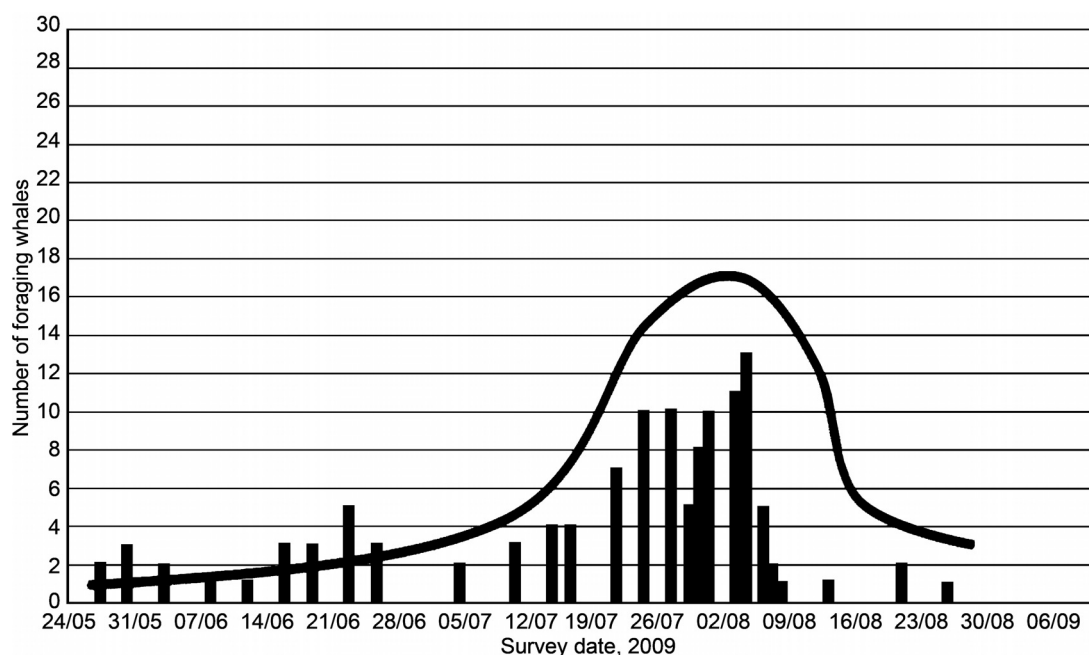

Fig. 6. Survey data of foraging whales from 2009, showing positive skew and leptokurtic distribution. Curve added to show how the data peaks around the peak data and just left of the peak.

Growth and reproduction of mysids

The growth and reproductive patterns of the four dominant mysid species (*Holmesimysis sculpta,* Tattersall, 1933; *Neomysis rayii,* Murdoch, 1885; *Telacanthomysis columbiae,* Tattersall, 1933; and *Columbiaemysis ignota*, Holmquist, 1892) were examined using the data collected from 2010–12. The mean length of individual mysids by 1mm size classes and the range of sizes were calculated (Figs 6–9). The length-frequency data were used to identify broods and growth, with the proportion of gravid females by species also quantified seasonally (Fig. 10). Mysid samples have gravid females in all seasons for the most numerically dominant species, but with distinct reproductive pulses. Brood production for many of the species present depends on warmer waters and increased productivity with juvenile release at the end of May, mid-June to early July and in late August to early September, with a fourth found for *H. sculpta* in November (Burnham, 2015). Average brood size for the species considered here is 50 (Feyrer, 2010a), with sexual maturity achieved in approximately 60 days (Mauchline, 1980; Wittman, 1984; Stelle, 2001; Mulkins *et al.,* 2002). Overwinter reproduction in *H. sculpta* represents a period where population recruitment, growth and maturation with removals from predators much reduced (Burnham, 2016).

DISCUSSION

The ability of gray whales to severely reduce benthic ampeliscid amphipod prey has been documented (Coyle
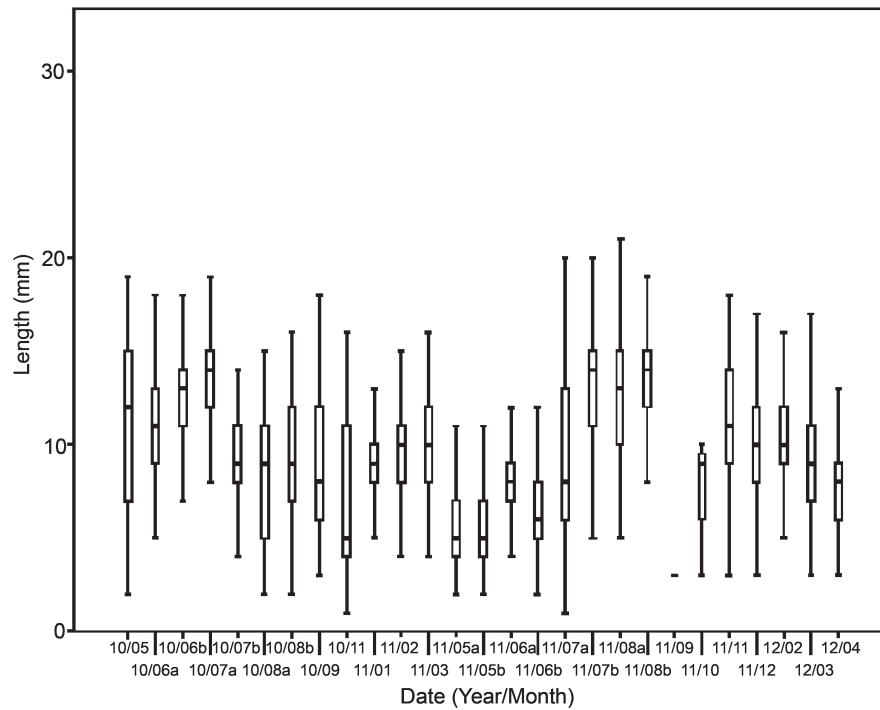
Fig. 7. Boxplot showing mean and standard deviation of body length of individuals in each sample over time for *Holmesimysis sculpta.*
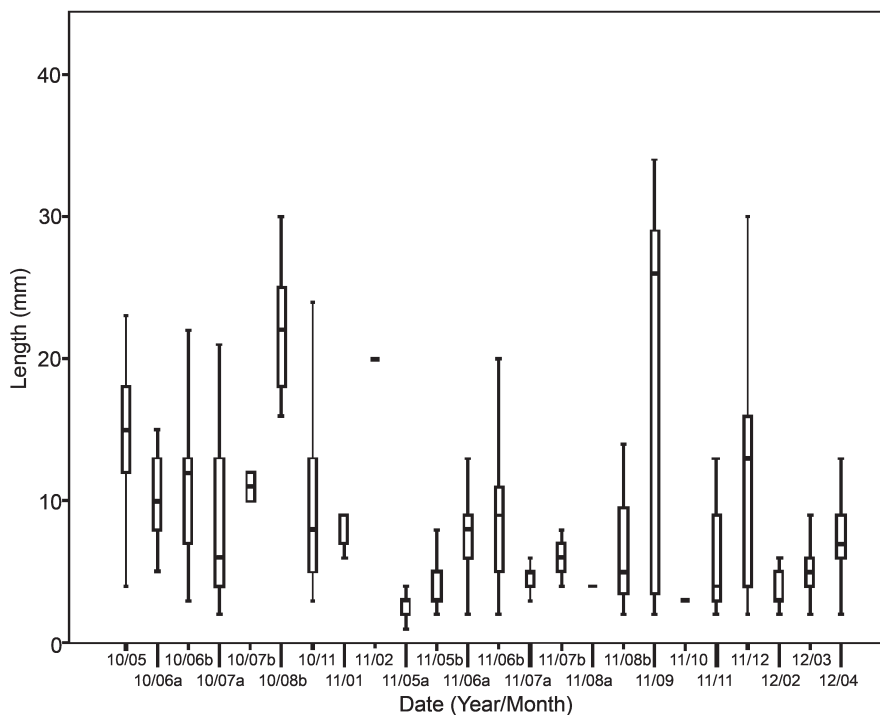

Fig. 8. Boxplot showing mean and standard deviation of body length of individuals in each sample over time for *Neomysis rayii.*

et al., 2007; Burnham and Duffus, 2016). Data presented here suggest that there is a similar capacity to depress epibenthic mysid prey although in this case, the prey populations have the capacity to recover. Predatory removal at sufficiently high levels will necessitate at least one summer season of high growth to re-establish swarms that again become a viable prey resource. The implication is that reprieve periods of low foraging for one to three years allowed mysid populations to rebuild, with three years required for reconstruction after the highest foraging years,

except in the case of 2011, which remained high after 2010 (see Table 1). This differs from amphipods, which have long maturation times and singular reproductive events for individuals. Life histories and loss of niche space has hindered the repopulation of infaunal prey, despite a release from annual predation (Burnham and Duffus, 2016).

Between 2004 and 2009 there were three sets of consecutive years with descending foraging, where a year of higher foraging is followed by a year of lower whale numbers. For each of these cycles the average and peak number of whales
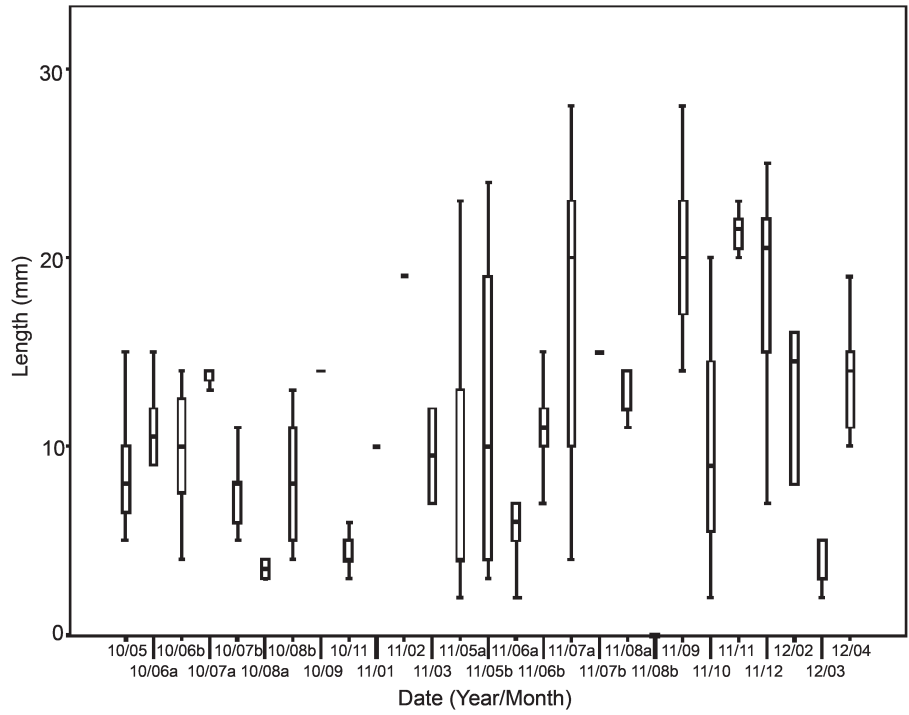
Fig. 9. Boxplot showing mean and standard deviation of body length of individuals in each sample over time for *Telacanthomysis columbiae.*
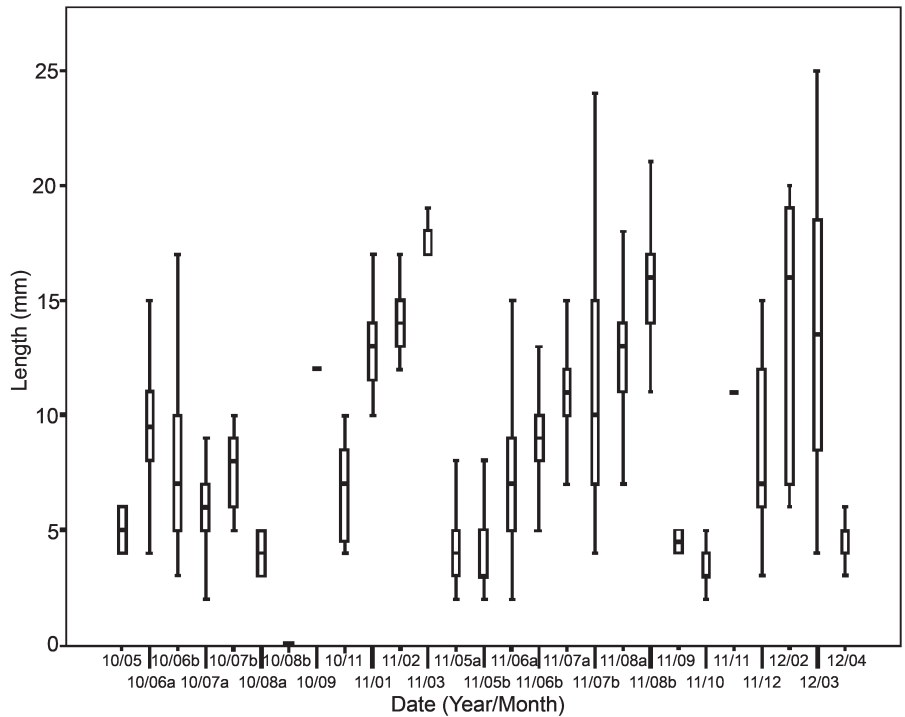

Fig. 10. Boxplot showing mean and standard deviation of body length of individuals in each sample over time for *Columbiaemysis ignota.*

for both the high and low year is approximately halved compared to the previous set (Fig. 2). The 2010 and 2011 data (i.e. two years of high numbers of foraging whales) are considered anomalous. Examination of external data revealed nothing unusual in the spring levels of primary production in this area at this time, or compared to coast-wide measurements (Feyrer, 2010b). This may support expanded prey populations, specifically those of *Holmesmysis sculpta*, the dominant species, which breeds overwinter and may have formed very large spring cohorts in the 2010–11 period.

In years where prey reserves do not exceed the 'threshold of interest' of predatory whales (see e.g. Bakun, 2006), lower foraging intensity can create a period of reprieve, allowing prey to reproduce with fewer losses. Once the resource recovers sufficiently, there will be a greater number of foraging whales in the following season(s). The cycling of prey population emulates 'predator-pit topography', where recovery, or 'breakout,' follows periods of prey 'refuge' and predator forced 'carnage' (Bakun, 2006). The data suggest a degree of 'boom-bust' cycling in foraging intensity,
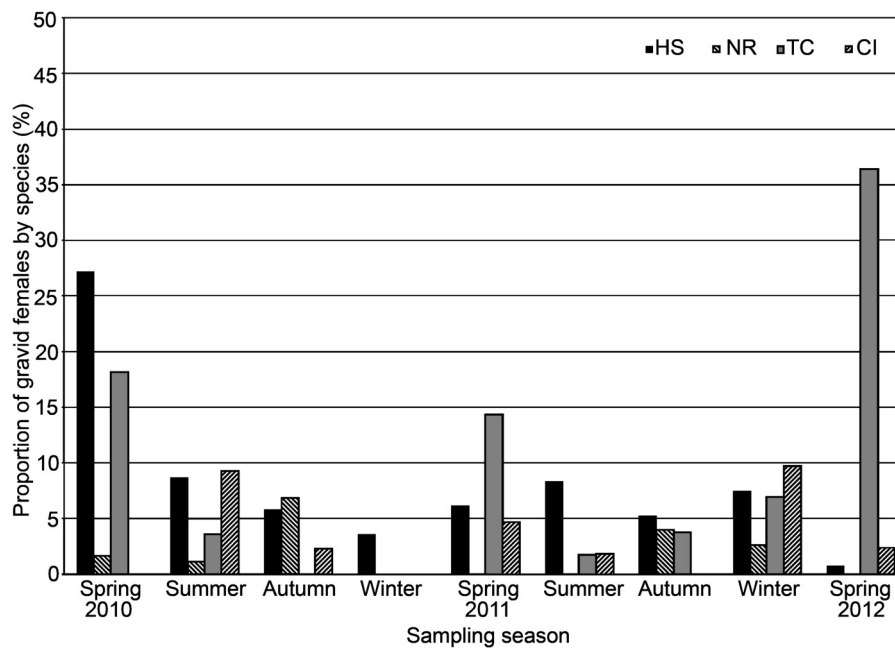
Fig. 11. Seasonal comparison of the percentage of gravid females per species for *H. sculpta* (HS), *N. rayii,*(NR) *T. columbiae* (TC) and *C. ignota* (CI). Spring: March, April, May; Summer: June, July, August; Autumn: September, October, November; Winter: December, January, February.

represented by the average number of whales foraging per survey (Table 1, Fig. 2) as well as the total annual number of foraging days that whales can be sustained by prey resources in Clayoquot Sound (Fig. 2). Years with intensified foraging compared to the global mean (boom) are followed by periods of reduced whale presence (bust) and so 1–3 years of 'refuge' for prey (see Table 1, Fig. 2). On only one occasion during the study period were there two consecutive high foraging years (2010 and 2011); and 2010 had the second highest mean value in the series behind the 2013 value (see Figs 2 and 3). These follow several years of depressed foraging. High foraging intensity was also seen in 2002 after the other extended low period (1999–2001; Fig. 2). Although number of whales does not have a direct relationship to prey presence, foraging pressure from whales has been established in this area as a reliable proxy for mysid abundance, both on a regional and site level. A foraging threshold on the prey-patch scale has been established, with feeding not seen to occur if mysid swarm density was below 2,300 mysids/m³ (Feyrer and Duffus, 2014).

Skew and kurtosis are unconventional means of assessing the trophic consequences of foraging by apex-predators, but they do describe the temporal procession of foraging pressure within a season. The expectation was for a platykurtic distribution, showing near consistent foraging intensity through a summer based on recurring mysid reproduction. Assuming that the peak foraging date would lag slightly behind mysid brood production, the expectation was a slight positive skew relative to a late summer maximum.

All years, with the exception of 2007, 2010 and 2011, showed a positive skew, where foraging intensity built towards the peak date and then declined rapidly. We suggest that this is likely to be a function of predation i.e. after the heaviest foraging period, mysid numbers collapsed. In the cases of negative skew and a low foraging intensity (e.g.

2007), it is hypothesised that whales may have moved into the site to search for prey but found little and thus moved to other locations. They may or may not return later in the season, pulled by growing stocks in this site, or pushed by mysid collapses in alternate sites. In the case of 2010 (see Fig. 3) and 2011, the negative skew may be attributed to the prey resource being high throughout the summer, which suggests successful foraging was still possible late into the season. These two years show unprecedented mysid presence following a three-year period of depressed foraging (Fig. 2). The whales foraging in Clayoquot Sound are part of a population subgroup, the Pacific Coastal Feeding Group (PCFG; Calambokidis *et al.*, 2010; IWC, 2010), with individuals showing high site fidelity to feeding locales, as well as also foraging in sites adjacent. In our case, it is likely whales assess the relative prey presence in areas extending from Puget Sound to the central British Columbia coast (Calambokidis *et al.*, 2010).

The platykurtic nature of the distributions obscured the pattern of skew somewhat, where several increases in foraging intensity within a season were seen (e.g. 2006, Fig. 4). The leptokurtic years (2000, 2001, 2007, 2008, 2009, 2012, 2013) show predation centred around the peak date. For years with a lower average number of foraging whales, this represents the exploitation of a single brood in an otherwise prey limited environment (e.g. 2009, Fig. 6).

No significant relationship between the number of whales foraging in the last two weeks of a season to the first fortnight of the following season was detected. The interplay between inter- and intra-seasonal demands may be masking any pattern. It is likely here we are comparing low whale numbers after prey has been reduced from a summer of foraging, and then spring-early summer the following year where mysid broods are yet to have become viable prey for gray whales after a winter of little reproduction or growth (Burnham, 2015). In the late spring/early summer mysids are

not an attractive resource to gray whales. The initial spring brood does not immediately form large dense swarms that attract whales, so this creates a period of repose for mysids. Broods produced later in the season show higher growth and swarm stabilisation and this attracts increased predation. Although mysid swarms matured as the season progressed, two months of foraging pressure in the mid-season on the progeny of two broods reduces mysid swarms by late summer, becoming once more insufficient as a prey resource. This deduction was supported by both the positive skew in the data and gray whale foraging peaking from mid to late summer (see Table 1). More detailed work on the life cycles of the mysid species present in the area, particularly the four species discussed here, have confirmed this (Burnham, 2015). However, for years with high numbers of foraging whales and a platykurtic distribution (e.g. 2010, 2011) the data suggested that prey was available in large swarms and sufficient biomass to attract whales for an extended period.

On both intra- and inter-seasonal scales, predator presence was linked to prey abundance, although the proliferation of prey was in turn linked to the previous year's predation. Gray whales have shaped their own prey abundance with mediation by the reproductive behaviour of the prey. Reproduction and recovery of mysid populations took place in periods of light foraging, heavy foraging and in the absence of foraging in a period of predator reprieve. These mixed processes each with their own success, go some way to buffer the effect of one summer's prey removals to the next.

The whales themselves have a buffer which allows them to easily move from poor quality to higher quality prey sites. Thus, it is quite likely that other sites to the north and south are linked. The interesting outcome of this study is that where there are physical situations similar to Clayoquot Sound along the west coast, some similar ecological narratives may be occurring. Not every headland/bay system with rocky reefs has records of foraging whales in recent times. This study proposes the possibility that whales may be a cause of longer-term ecological change to these sites where predatory behaviour exceeds prey resilience. Longer time spans of observation and prey analysis are necessary to further this study's findings.

ACKNOWLEDGEMENTS

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