Relating gray whale abundance to environmental variables

by

Chelsea Faye Garside
B.Sc., University of Victoria, 2001

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ABSTRACT

The abundance of gray whales along the coast of Flores Island, BC, varies on an annual basis. This thesis searches for a relationship between gray whale abundance in this area and environmental forcing factors. Regression analysis was used to search for relationships, using gray whale abundance as the dependent variable and sea-surface temperature, salinity, wind speed, upwelling indices and hours of bright sunlight. Independent variables were also lagged against gray whale abundance to search for time lags between variables. When combine in a multiple regression model, wind speed and upwelling lagged two years explained 89.6% ($p = 0.004$) of the variance in gray whale abundance. A possible pathway for this relationship may exist through local kelp populations, which have the ability to affect gray whale prey abundance.

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Chapter 1 – Introduction

The relationships between environmental variables and marine mammal abundance are an important part of the study of foraging habitats of marine mammals. An understanding of these relationships is essential for understanding the importance of particular ecological processes or habitat features in influencing marine mammal abundance over specific spatial and temporal scales. This study is intended to address the current gap in knowledge that exists in the understanding of how gray whale abundance is related to or influenced by environmental variables. Other studies have examined the links between marine mammals and environmental variables (Benson *et al.* 2002, Croll *et al.* 2005, Keiper *et al.* 2005, Laidre *et al.* 2004), but none have examined the relationships for a coastal species such as the gray whale. As well, most studies have used broad scale oceanographic and cetacean abundance data, while this study will attempt to demonstrate scale-coupling by linking broad scale oceanographic data to fine scale gray whale data.

Gray whale biology

Gray whales may be differentiated from other baleen whales by colour (varying from light to dark grey), lack of a true dorsal fin, possession of 8-14 dorsal "knuckles", short and rather stocky body with a maximum length of 13-14m, and baleen which is thicker and coarser than all other baleen whales (Evans & Raga 2001, Jones and Swartz 2002).

The gray whale is generally slow moving, thus harbouring one of the largest external parasite loads of any cetacean (Jones & Swartz 2002). The parasite load is generally composed of barnacles and whale lice. The barnacles settle as nauplii onto the whale and feed from the water column, while the lice feed on the whales' dead or damaged skin, and will often inhabit wounds or folds/pleats of skin (Jones and Swartz 2002). These parasites may be symbiotically removed by schools of fish in the breeding lagoons of Baja California (these are generally topsmelt – *Atherinops affinis*) (Jones and Swartz 2002).

Gray whales mate between November and December, with gestation lasting 11-13 months (Evans & Raga 2001, Jones & Swartz, 2002). The resultant calves are born between December and early March, with the median birth date being January 27 (Jones & Swartz 2002). Gray whale mother and calf pairs are the last to make the migration northward towards the summer feeding grounds. Females enjoy an especially strong bond with their

young, and will defend them fiercely against threats such as killer whales (Jones & Swartz 2002). The lactation period lasts approximately 7 months, and as calves begin to forage during the latter part of this period, they thus gain familiarity with foraging while they are still with their mother (Evans & Raga 2001, Jones & Swartz, 2002).

Gray whales may forage infrequently on planktonic prey around Baja California, but most early feeding is believed to occur outside the breeding lagoons (Evans & Raga 2001). Gray whales' foraging is limited to waters 4-120m in depth (Jones & Swartz 2002). They are plastic foragers, taking prey at the surface, in the water column, and in the benthos (Evans & Raga 2001), although they mainly feed at the bottom (Jones & Swartz 2002). In the feeding grounds of the Bering and Chukchi Seas, most foraging is on benthic-dwelling amphipods, which occur in extremely dense concentrations, allowing the whales to feed heavily in these areas (Jones & Swartz 2002). The manner in which gray whales feed on the amphipods makes them a cetacean most active in moulding feeding areas; using suction created through the use of the tongue, they excavate pits in the ocean floor, sucking water, mud and prey into their mouths, then pushing out the water and mud, while the prey are contained within the mouth by the baleen (Jones & Swartz 2002).

Gray whales belonging to the northeastern Pacific population may travel up to 20,000 km during migration if they make the full-length journey between the Gulf of California and Alaska (Evans & Raga 2001, Jones & Swartz, 2002). Some whales will not make the full migration and may stop off at locations along the migration route, feeding in these places before heading south when the return migration is in progress. This is the case with the whales whose annual abundance was examined in this study.

The fact that gray whales perform one of the longest migrations of any marine mammal (Jones & Swartz, 2002) may be a possible explanation for why they take advantage of so many different types of prey; on such a long migration, they have to make use of what resources are available. This characteristic could also protect gray whales against major population crashes; if they are able to exploit multiple resources, then the possibility of a crash in one prey population would be less of a problem than for more specialised predators.

The northeastern Pacific population of gray whales has recently been estimated at 26,000, which is believed to be at or slightly over the estimated historical population of

15,000-24,000; this has led researchers to conclude that the population stability or slight decreases may be forecast for the future (Jones & Swartz 2002).

Marine mammals and environmental variables

Although relationships between environmental variables and biological entities may be obscured for different reasons, there are some variables that directly or indirectly affect said entities. For example, sunlight has a direct effect on the amount of chlorophyll produced by phytoplankton; more sunlight generally equals more chlorophyll, barring the effects of other interfering variables. This direct effect may be referred to as environmental forcing, in that the sunlight is 'forcing' an effect in terms of chlorophyll production. The variable inducing the environmental forcing may be referred to as an environmental forcing factor, which in this case would be sunlight.

Environmental variables, or forcing factors, are those variables that drive marine production at very low trophic levels. For example, upwelling has been shown to influence the production of low trophic-level euphausiids, which in turn influence the local abundance of higher trophic level marine mammals (Croll *et al.* 2005). Upwelling occurs when water is forced offshore by shore-parallel winds via the Coriolis force. The "pulling away" of water from the coast results in a flow of bottom water upwards to the surface to fill the loss – this is upwelling. With the upwelled water comes nutrients, both micro and macro, the abundance of which can lead to increases in the production of organisms that use those nutrients, such as phytoplankton (Lalli & Parsons 1997).

Environmental forcing factors may directly affect the distribution of marine mammals, as animals are reliant on their prey to meet their energetic requirements. Changes in environmental variables can affect prey distribution, quantity and availability (see for example Croll *et al.* 2005). In some cases, specific environmental variables may describe particular foraging habitats used by marine mammals (Laidre *et al.* 2004), rather than be indicative of a relationship between environmental forcing and the organism. Either way, relationships between environmental variables and marine mammal presence or abundance allow for the definition of what makes for good foraging habitat.

Several studies have examined the effects of environmental variables on marine mammal distributions. Large numbers of foraging blue whales (*Balaenoptera musculus*)

have been observed off the coast of California when euphausiids are aggregated in the area due to the effects of bottom topography and seasonal upwelling (Croll *et al.* 2005). The authors rely on a simplified time series approach, where graphs of number of whales observed per trip, chlorophyll a, primary production, SST and upwelling index are shown in sequence. A relationship between upwelling and whale abundance appears to be present, although there are no statistical quantifications of any relationship between these variables. Rorquals are also hypothesised to respond to oceanographic forcing on broad spatial scales, particularly during oceanic events such as El Niño, which are suspected to significantly affect zooplankton prey distribution (Benson *et al.* 2002). Thus it is apparent that broad-scale oceanographic conditions may affect the prey of marine mammals to the extent that it causes changes in their abundance and spatial distribution.

Keiper et al. (2005) studied the occurrence of marine mammals along the coast of central California in relation to environmental variables, as well as the availability of prey species. The authors used multiple logistic regression to test for relationships between the abundance of various marine mammal species and environmental variables, and then used principal components analysis to further investigate these relationships. Distributions of sperm whales recorded at broad spatial scales have also been related to environmental variables using principal components analysis (Jaquet & Whitehead 1996). Other authors have taken a more technological approach, employing new technologies such as geographic information systems (GIS) to organise data and search for links between environmental variables and the distributions of organisms (see for example Laidre *et al.* 2004, Littaye *et al.* 2004, Moses & Finn 1997). The arrangement of the data in a visual, spatial pattern as it is in GIS, may facilitate the identification of relationships between variables. However, this approach does not provide any statistical information regarding the strength of relationships between variables or the amount of variance in one variable explained by another; the use of statistical analyses is necessary to achieve these ends.

As well as variable ocean conditions, there are also processes that occur at broad spatial scales, which have the potential to affect the abundance and availability of marine mammal prey species. These examples indicate that it is possible to link marine mammal abundance with environmental variables at single spatial and temporal scales. This study

will extend this research to gray whales in order to assess the effects of environmental variables on local gray whale abundance.

Broad scale disturbances – Regime shifts, El Niño/La Niña and the North Pacific Current

Oceanographic disturbances occur at a myriad of spatial scales, but those with broad spatial effects are expected to affect the greatest variety of organisms overall. The effects of such processes may also be observed in biological data series such as gray whale abundance. Research has shown that these disturbances can be transferred up the food web from lower to higher trophic levels (Benson *et al.* 2002, Chavez *et al.* 2003, PICES 2004, PICES 2005). Although it is not a specific objective of this study to identify specific events occurring at broad scales, the events may provide some explanation for variations in the number of whales observed, and thus will be considered in such a context.

Perhaps one of the broadest spatial scales at which oceanographic processes might be experienced is that of the northeastern Pacific Ocean. Changes to the dominant current regime in this area could affect the abundance and distribution of a wide variety of organisms, particularly those that rely on currents to disperse their progeny. Nutrient supply could also be affected, as could SST values, in turn affecting organisms such as phytoplankton. Changes in abundance of low-trophic level organisms due to changes in nutrient supply and SST could then be passed up the food web to higher trophic level predators. Broad-scale changes in northeastern Pacific current circulation have been recorded by the ARGO drogued drifter programme (Freeland & Cummins 2005).

Regime shifts occurred in the northeastern Pacific in 1976/77, 1989 and 1998 (PICES 2005), and have been observed to affect organisms at multiple trophic levels of the food web (Anderson & Piatt 1999, Hare & Mantua 2000). Changes in oceanographic regimes may alter the basic environmental conditions, which in turn can affect different organisms in different ways. Fluctuations in the abundance of some species appear to be closely linked to regime shifts. Abundance and recruitment of some species, such as barnacles, halibut and flounder may be increased (Connolly & Roughgarden 1999, Bailey & Picquelle 2002), while the abundance of others, such as marine birds, shrimp and capelin may be severely decreased (Agler *et al.* 1999, Anderson *et al.* 1997). It is also possible that different species may dominate different regimes. Chavez et al. (2003) discuss possible regime shifts where eastern

Pacific 'cool' regimes are dominated by anchovies, while 'warm' regimes are dominated by sardines. In turn, abundance of larger fish such as salmon and tuna are also affected. This suggests that species assemblages may also change depending on the regime, which in turn has the potential to affect their predators (Benson & Trites 2002), including higher trophic level organisms such as gray whales and other marine mammals.

El Niño/La Niña have the ability to affect species abundance by reducing upwelling in areas where seasonal upwelling is an important ecosystem process, leading to poor recruitment of juveniles (Sugimoto *et al.* 2001). Reductions in upwelling can disrupt phytoplankton production as nutrients are depleted; examples of this have occurred over the continental shelf off the British Columbia coast during past ENSO events (Whitney & Welch 2002). This theoretically leads to a reduction in phytoplankton available to zooplankton, and thus zooplankton production, and then a reduction in marine mammal prey populations at higher trophic levels.

Gray whale research in the northeast Pacific

Traditionally, research on gray whale use of foraging habitat has focused mainly on primary and secondary feeding areas; see for example Clarke *et al.* (1989), Highsmith & Coyle (1992), and Moore *et al.* (2003). As gray whale populations rebounded from historically depressed levels caused by whaling, whales began to utilise habitat in areas where they were previously not observed. These so-called 'tertiary' foraging areas are located along the gray whale migration route between calving grounds in Baja California, Mexico, while primary and secondary feeding areas are located in the Bering and Chukchi Seas (Kim & Oliver 1989).

Some gray whales 'stop over' in mid-migration to take advantage of the prey resources in the tertiary feeding areas (Murison *et al.* 1984, Calambokidis *et al.* 2002, Newell & Cowles 2006), staying for variable lengths of time, presumably depending on the quality, quantity and life history stage of prey available in each area. Newell & Cowles (2006) found that gray whales exploiting tertiary foraging areas along the Oregon coast returned to the same areas year after year, and that these whales exhibited poor body condition when local mysid prey were scarce or reproducing poorly. Calambokidis *et al.* (2002) also identified specific whales that returned annually to forage in tertiary feeding grounds. They also noted

that some whales exhibited higher site fidelity than others; those observed along the west coast of Vancouver Island had a 70-100% re-sighting rate, indicating that the same individuals were returning year after year to the same area.

Gray whales are known to be very plastic foragers, with prey items changing by habitat area and between primary, secondary and tertiary foraging areas (Moore *et al.* 2003). In the tertiary foraging areas, gray whales have been observed to either exploit several different prey resources, or only planktonic prey resources, as observed in their primary and secondary foraging areas where they forage on the benthos (Murison *et al.* 1984, Kim & Oliver 1989, Dunham and Duffus 2001, Dunham and Duffus 2002, Moore *et al.* 2003, Stelle *et al.* 2008). They are also known to decimate prey areas to levels where foraging is assumed to no longer be efficient, at which point they then move on to areas where prey are believed to be more abundant (Kim & Oliver 1989, Moore *et al.* 2003). In a study completed in a tertiary foraging area, Stelle *et al.* (2008) note that foraging gray whales dove frequently (26.7 dives/hour), and made mostly short dives (mean = 2.24 minutes), indicating that these whales were foraging on planktonic prey rather than benthic prey.

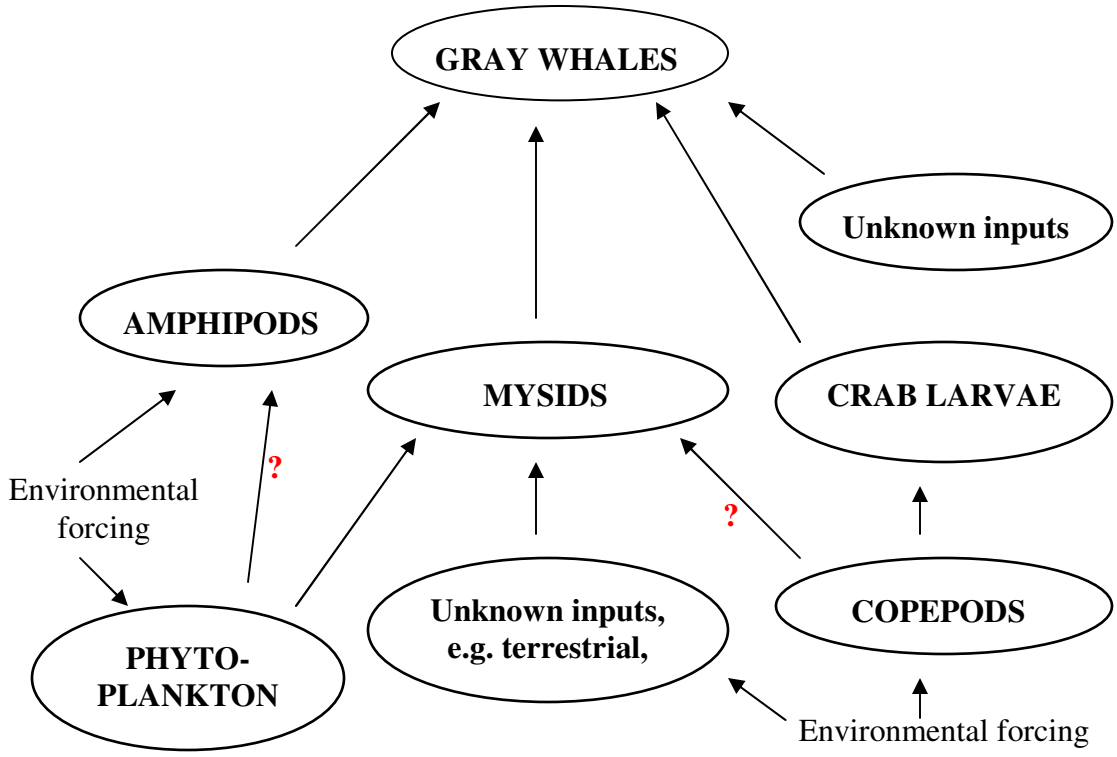
In contrast to the primary foraging areas where gray whales feed primarily on benthic organisms, the main prey item of gray whales along the central west coast of Vancouver Island and the central BC coast appears to be mysids, also known colloquially as opossum shrimp. These organisms have been noted as the main prey item in several different studies completed over about 24 years (Murison *et al.* 1984, Dunham and Duffus 2001, Stelle 2001, Stelle *et al*. 2008), indicating that gray whale use of this prey item in these areas has been relatively consistent over time. This relationship between mysids and gray whales may also be related to the presence of kelp. All of the above studies noted that the main genus present was *Holmesimysis*, which has been associated with kelp (Holmquist 1979 cited in Murison *et al.* 1984, Turpen *et al*. 1994). In fact, Stelle (2001) noted that gray whales did not frequent areas with little kelp as much as areas with large amounts of kelp present. Turpen *et al*. (1994) believe that *Holmesimysis* abundance may be closely linked to kelp abundance, and winter storms that uproot kelp and wash it away may be responsible for decreases in localised mysid abundance.

Present foci in gray whale research include abundance assessments, physiology research,and behaviour studies, with few publications examining the role of tertiary foraging

areas in the distribution of northeastern Pacific gray whales. Although the total number of whales using the entire tertiary feeding area is unknown, Calambokidis *et al.* (2002) used photographic identification techniques to estimate that at least 155 whales have been identified using tertiary habitat areas. Although this group is small, the data only cover small, discrete study areas, and there is potential for much greater numbers of whales to use this habitat. Thus, this area provides important habitat for some gray whales and as such warrants further investigation in terms of how gray whale abundance in these tertiary areas can change in relation to changes in environmental variables.

The gray whale food web

In comparison to the food chain of toothed whales such as killer whales, the plankton-based food chain of baleen whales is relatively short, likely involving three or four trophic levels. In the study area, gray whales have been observed to feed on a variety of prey items, as mentioned above. The prey most commonly consumed in this area are mysids, hyperbenthic crustaceans that aggregate in swarms above rocky areas or piles of stones, and in areas where kelp is present (Patterson 2004). See Fig. 1 for a simplified diagram of the gray whale food web, including forcing factors, phytoplankton, zooplankton and gray whales.



Environmental forcing may include, but is not limited to: SST, salinity, wind speed, upwelling, sunlight, or wave height. All populations of plankton are assumed to be affected by sinking and mixing (immigration and emigration).

Figure 1. A simplified diagram of the gray whale food web in the study area, created from information provided in Patterson (2004) and Dunham & Duffus (2002). Note that question marks (?) indicate unknown or hypothesised relationships.

Scale coupling

The consideration of scale in ecology has been defined as an area that is extremely important but is often neglected in traditional ecological research (Levin 1992). Relating data at different spatial scales allows for linking processes over broad geographic areas to those over fine geographic scales; however, it is rare that data are collected at multiple spatial scales for one particular study (Powell 1989, Schneider 2001). The concept of scale coupling is very simple; it involves relating data at one spatial scale to data at another spatial scale. For example, a broad scale process might create a fine scale response or vice versa. In this study, broad scale environmental data will be examined in relation to fine-scale gray whale

abundance to search for relationships that might ameliorate the understanding of how broad scale processes can elicit fine scale responses. Although the concept of scale coupling is relatively simple, the creation of models including upper-trophic level predators is considered difficult, as the relationships between environmental variables and such predators are often ephemeral in space and time (DeYoung *et al.* 2004).

It is also important to note that many relationships between events at different scales may be affected by time lags, which are an important factor to consider when investigating the relationships between environmental forcing factors and marine mammals.

Time lags

Time lags are periods of time that pass between a stimulus and a response (Duarte 1990), and have been observed between environmental forcing factors and organisms at higher trophic levels (Andrade & Garcia 1999). Time lags may vary in length and by trophic level, with lags of hours to days reported for phytoplankton response to nutrients and sunlight (Duarte 1990), to a 9-year time lag between a change in SST and a response by elephant seal populations (Weimerskirch *et al.* 2003).

An analysis of the role of time lags in this study is important to the understanding of the dynamics of interactions between gray whales, their prey and influences of environmental forcing factors. Time lags should exist between the stimulus (environmental forcing factors) and the response (gray whale abundance). In the case of the gray whale food web, energy must pass from stimuli such as sunlight and nutrients to phytoplankton or algae to zooplankton prey species and then to gray whales. Due to a lack of detailed information on the life history and foraging habits of prey species in the study area, the presence or absence and length of any time lags in this relationship are currently unknown. However, it is important to consider the presence of time lags, as ignoring them can obscure relationships that are integral to the understanding of a particular food web, and thus of the behaviour exhibited by foraging gray whales.

Rationale for this study

Past research on gray whales in Clayoquot Sound revealed that summer gray whale abundance varies on an annual scale (Patterson 2004, Dunham & Duffus 2001). The

observation of this variation leads to questions regarding the controls on local summer gray whale abundance in the area. My main interest was to investigate the relationships between events (stimuli) occurring at a lower trophic level and effects (responses) occurring at a higher trophic level. It is likely that environmental variables indirectly affect gray whale abundance in the study area, although the pathways through which the effects are manifested are not currently well understood. Identification of relationships between variables, time lags, and the possibility of scale coupling will advance scientific knowledge regarding gray whale foraging in our study area and in general.

Research questions

Questions that will drive this study:

1. What role do environmental variables play in influencing the relative abundance of gray whales in the study area?
2. Can these environmental variables, or forcing factors, be statistically related to gray whale abundance?
3. Are time lags present in any relationships between forcing and forced parts of the food web and, if present, how long are they?
4. To what extent do the environmental data collected at a broad spatial scale explain gray whale data collected at a fine spatial scale?

Environmental variables influence whales indirectly by altering the abundance of prey items such as mysids. This study is intended to advance current knowledge of the extent to which higher levels of the food web react to bottom-up influences (environmental variables), and over which time scales such a reaction might occur. In the analyses presented here, it is assumed that foraging gray whale abundance acts as a proxy for general prey abundance, as it is fairly simple to recognize what gray whales are consuming based on the behaviour of the whales the prey habitat in that area and the area where they are foraging (Dunham & Duffus 2002).

Discussion of the questions: how they will be answered

To address the first objective, changes in gray whale abundance will be statistically related to environmental variables in order to better understand the relationship between environmental forcing parameters and responses higher up the food web. The use of basic, easily measurable and available data makes this study a simple way to investigate the dynamics between gray whales and the factors that influence their summer abundance in the study area.

The second objective of this study is to investigate the time scales over which gray whales respond to environmental variables, if at all. This objective will be met by analysing data aggregated at multiple temporal scales, which is purely an exploratory method for searching for time lags. Testing in this manner cannot confirm the total absence of time lags; rather it can only confirm presence or absence over the time period tested. Therefore, I will only be able to say whether or not gray whale abundance is related to environmental variables at the time scales and over the time lags I choose to test here.

The third objective is based on the concept of scale coupling, where data at one spatial scale are statistically or theoretically connected to other data at another spatial scale. In this study, I will attempt to statistically relate broad spatial scale data from oceanographic and environmental variables to the dependent studied at a fine spatial scale. All three objectives can be met through the use of regression and multiple regression analysis. There are several important assumptions made during the use of this type of statistical analysis, which are discussed in detail in the *Methods* section of the next chapter.

Literature Cited

Agler, B.A., S.J. Kendall, D.B. Irons, & S.P. Klosiewski. 1999. Declines in marine bird populations in Prince William Sound, Alaska coincident with a climatic regime shift. *Waterbirds,* **22**(1): 98-103.

Anderson, P.J., J.E. Blackburn, and B.A. Johnson. 1997. Declines of forage species in the Gulf of Alaska, 1972-1995, as an indicator of regime shift. *In* Forage Fishes in Marine Ecosystems.; Int. Symp. on the Role of Forage Fishes in Marine Ecosystems, Anchorage, Alaska (USA), 13-16 Nov 1996. *Edited by* American Fisheries Society, Fairbanks, Alaska. pp. 531-543.

Anderson, P.J. & J.F. Piatt. 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Marine Ecology Progress Series,* **189**: 117-123.

Andrade, H.A. & C.A.E. Garcia. 1999. Skipjack tuna fishery in relation to sea surface temperature off the southern Brazilian coast. *Fisheries Oceanography,* **8**(4): 245-254.

Bailey, K.M. & S.J. Picquelle. 2002. Larval distribution of offshore spawning flatfish in the Gulf of Alaska: Potential transport pathways and enhanced onshore transport during ENSO events. *Marine Ecology Progress Series,* **236**: 205-217.

Benson, A.J. & A.W. Trites. 2002. Ecological effects of regime shifts in the Bering Sea and eastern North Pacific Ocean. *Fish and Fisheries,* **3**(2): 95-113.

Benson, S.R., D.A. Croll, B.B. Marinovic, F.P. Chavez, & J.T. Harvey. 2002. Changes in the cetacean assemblage of a coastal upwelling ecosystem during El Nino 1997-98 and La Nina 1999. *Progress in Oceanography,* **54**(1-4): 279-291.

Calambokidis, J., J.D. Darling, V. Deecke, P. Gearin, M. Gosho, W. Megill, C.M. Tombach, D. Goley, C. Toropova, & B. Gisborne. 2002. Abundance, range and movements of a feeding aggregation of gray whales (*Eschrichtius robustus*) from California to southeastern Alaska in 1998. *Journal of Cetacean Research and Management,* **4**(3): 267-276.

Chavez, F.P., J. Ryan, S.E. Lluch-Cota, & C.M. Niquen. 2003. From anchovies to sardines and back: multidecadal change in the Pacific Ocean. *Science,* **299**(5604): 217-221.

Clarke, J.T., S.E. Moore, & D.K. Ljungblad. 1989. Observations on gray whale *Eschrichtius robustus* utilization patterns in the northeastern Chukchi Sea, Arctic Ocean July-October 1982-1987. *Canadian Journal of Zoology,* **67**(11): 2646-2654.

Connolly, S.R. & J. Roughgarden. 1999. Increased recruitment of northeast Pacific barnacles during the 1997 El Nino. *Limnology and Oceanography,* **44**(2): 466-469.

Croll, D.A., B. Marinovic, S. Benson, F.P. Chavez, N. Black, R. Ternullo, & B.R. Tershy. 2005. From wind to whales: trophic links in a coastal upwelling system. *Marine Ecology Progress Series,* **289**: 117-130.

DeYoung, B., M. Heath, F. Werner, F. Chai, B. Megrey, & P. Monfray. 2004. Challenges of modeling ocean basin ecosystems. *Science,* **304**(5676): 1463-1466.

Draper, N.R. & H. Smith. 1998. Applied regression analysis, 3rd ed. Wiley Interscience: New York, USA. 736 p.

Duarte, C.M. 1990. Time lags in algal growth: generality, causes and consequences. *Journal of Plankton Research,* **12**(4): 873-883.

Dunham, J.S. & D.A. Duffus. 2001. Foraging patterns of gray whales in central Clayoquot Sound, British Columbia, Canada. *Marine Ecology Progress Series,* **223**: 299-310.

Dunham, J.S. & D.A. Duffus. 2002. Diet of gray whales (*Eschrichtius robustus*) in Clayoquot Sound, British Columbia, Canada. *Marine Mammal Science,* **18**(2): 419-437.

Evans, P.G.H &S J.A. Raga. 2001. Marine mammals: Biology and Conservation. Kluwer Academic/Plenum Publishers: New York, USA. 630 p.

Freeland, H.J. & P.F. Cummins. 2005. Argo: A new tool for environmental monitoring and assessment of the world's oceans, and example from the N.E. Pacific. *Progress in Oceanography,* **64**: 31-44.

Hair, J.F.J., R.E. Anderson, R.L. Tatham, & W.C. Black. 1998. Multivariate data analysis, 5th edition. Prentice Hall: Upper Saddle River, NJ, USA. 730 p.

Hare, S.R. & N.J. Mantua. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Progress in Oceanography,* **47**(2-4): 103-145.

Highsmith, R.C. & K.O. Coyle. 1992. Productivity of Arctic amphipods relative to gray whale energy requirements. *Marine Ecology Progress Series,* **83**(2-3): 141-150.

Jaquet, N. & H. Whitehead. 1996. Scale-dependent correlation of sperm whale distribution with environmental features and productivity in the South Pacific. *Marine Ecology Progress Series,* **135**(1-3): 1-9.

Jones, M.L. & S.L. Swartz. 2002. Gray whale: *Eschrichtius robustus*. *In:* Encyclopaedia of marine mammals. Perrin, W.F., B. Würsig, and J.G.M. Thewissen (eds.). Academic Press: San Diego, USA. p.524-536.

Kim, S.L. & J.S. Oliver. 1989. Swarming benthic crustaceans in the Bering and Chukchi seas and their relation to geographic patterns in gray whale feeding. *Canadian Journal of Zoology,* **67**(6): 1531-1542.

Laidre, K.L., M.P. Heide-Jorgensen, M.L. Logdson, R.C. Hobbs, P. Heagerty, R. Dietz, O.A. Jorgensen, & M.A. Treble. 2004. Seasonal narwhal habitat associations in the high Arctic. *Marine Biology,* **145**(4): 821-831.

Levin, S.A. 1992. The problem of pattern and scale in ecology. *Ecology,* **73**(6): 1943-1967.

Littaye, A., A. Gannier, S. Laran, & J.P.F. Wilson. 2004. The relationship between summer aggregation of fin whales and satellite-derived environmental conditions in the northwestern Mediterranean Sea. *Remote Sensing of Environment,* **90**(1): 44-52.

Mickey, R.M., O.J. Dunn, & V.A. Clark. 2004. Applied statistics: Analysis of variance and regression. Wiley Interscience: Hoboken, NJ, USA. 448 p.

Moore, S.E., J.M. Grebmeier, & J.R. Davies. 2003. Gray whale distribution relative to forage habitat in the northern Bering Sea: Current conditions and retrospective summary. *Canadian Journal of Zoology,* **81**(4): 734-742.

Moses, E. & J.T. Finn. 1997. Using geographic information systems to predict north Atlantic right whale (*Eubalaena glacialis*) habitat. *Journal of Northwest Atlantic Fisheries Science,* **22**: 37-46.

Murison, L.D., D.J. Murie, K.R. Morin, and de Silva Curiel, J. 1984. Foraging of the gray whale along the West coast of Vancouver Island, British Columbia. *In* The gray whale *Eschrichtius robustus*. *Edited by* M.L. Jones, S.L. Swartz and S. Leatherwood. Academic Press, Inc., Orlando, FL, USA. pp. 451-463.

Newell, C.L., and T.J. Cowles. 2006. Unusual gray whale *Eschrichtius robustus* feeding in the summer of 2005 off the central Oregon coast. *Geophysical Research Letters*, 33: L22S11.

North Pacific Marine Science Organisation (PICES). 2005. Report of the study group on fisheries and ecosystem responses to recent regime shifts. No. 28, North Pacific Marine Science Organisation (PICES), Sidney, BC, Canada.

North Pacific Marine Science Organisation (PICES). 2004. Marine Ecosystems of the North Pacific. No. 1, North Pacific Marine Science Organisation (PICES), Sidney, BC, Canada.

Patterson. H. M. 2004. Small-scale distributions and dynamics of the mysid prey of gray whales (*Eschrichtius robustus*) in Clayoquot Sound, British Columbia, Canada. M.Sc. University of Victoria, Victoria BC Canada.

Powell, T.M. 1989. Physical and biological scales of variability on lakes, estuaries and the coastal ocean. *In* Perspectives in ecological theory. *Edited by* J. Roughgarden, R.M. May and S.A. Levin. Princeton University Press, Princeton, NJ, USA. pp. 157-176.

Schneider, D.C. 2001. The rise of the concept of scale in ecology. *Bioscience,* **51**(7): 545-553.

Stelle, L.L., W.M. Megill, and M.R. Kinzel. 2008. Activity budget and diving behaviour of gray whales (*Eschrichtius robustus*) in feeding grounds off coastal British Columbia. *Marine Mammal Science*, **24**(3): 462-478.

Sugimoto, T., S. Kimura, & K. Tadokoro. 2001. Impact of El Nino events and climate regime shift on living resources in the western North Pacific. *Progress in Oceanography,* **49**(1-4): 113-127.

Tabachnick, B.G. & L.S. Fidell. 1983. Using multivariate statistics. Harper & Row: New York, NY, USA. 509 p.

Weimerskirch, H., P. Inchausti, C. Guinet, & C. Barbraud. 2003. Trends in bird and seal populations as indicators of a system shift in the Southern Ocean. *Antarctic Science,* **15**(2): 249-256.

Whitney, F.A. & D.W. Welch. 2002. Impact of the 1997-1998 El Nino and 1999 La Nina on nutrient supply in the Gulf of Alaska. *Progress in Oceanography,* **54**(1-4): 405-421.

Chapter 2 – Gray whales and environmental variables: A regression analysis approach

Introduction

Interactions between the atmosphere and ocean may effect changes in broad spatial scale oceanography on temporal scales from days to decades (Greene & Pershing 2000, McGowan *et al.* 2003). These alterations of oceanographic parameters including sea surface temperature (SST), salinity, and upwelling have the potential to affect the distribution and abundance of organisms at many trophic levels of the food web. Such is the case of oceanic regime shifts, where organisms at multiple trophic levels and even entire ecological communities may be affected by changes to oceanographic and environmental variables on a decadal time scale (Anderson *et al.* 1997, Anderson 2000, Benson & Trites 2002, Hyrenbach & Veit 2003, PICES 2005). Temporally shorter environmental events such as El Niño-Southern Oscillation (ENSO) events which also alter broad scale oceanography also have the ability to affect organisms at multiple trophic levels (Sydeman & Allen 1999, Bailey 2000, Kaeriyama *et al.* 2004, Miller & Sydeman 2004, Edwards & Hernandez-Carmona 2005). Relationships between organisms and environmental variables may also be present at times when no broad scale environmental events are present; these have been noted at multiple trophic levels (Johnson *et al.* 1986, Jaquet & Whitehead 1996, Andrade & Garcia 1999, Clark & Hare 2002, Kinlan 2003, Croll *et al.* 2005). Biological responses to changes in oceanographic variables over broad spatial scales are expected to have the potential to affect top predators at higher trophic levels even over fine spatial scales over a small geographic area. Although the temporal scales to be examined in this study are much shorter than the multi-decadal scale of regime shifts, these longer-term changes in ocean conditions may have the ability to impact organisms over the shorter time scales investigated here.

Assessing the affect of oceanographic phenomena on biota is not simple or straightforward for several reasons. First, some organisms may respond to a stimulus in different ways, or one may respond and another other not at all, depending on their life history and position in the food web. Second, some organisms may respond in a manner that is difficult to interpret, or in a manner which is unidentifiable as a response given current scientific knowledge. Third, the connections between atmosphere and ocean are not well understood, in terms of atmospheric forcing of changes in oceanography over multiple

temporal scales. Fourth, the pathways though which organisms may be affected by oceanographic change may not always be simple to identify or comprehend. Fifth, the temporal or spatial scale at which an organism responds to oceanographic forcing may not be the scale at which the problem is being examined by the researcher and thus will not be identifiable as a pathway. Overall, this is why few studies have been able to both link oceanographic conditions to a particular organism and identify the pathway or mechanism by which the oceanography affects the organism. This is particularly true for marine mammals such as whales, whose prey patches can be variable in time and space; see for example (Benson & Trites 2002, Benson *et al.* 2002, Croll *et al.* 2005). Sixth, it has been noted that relationships between data series of abundance of organisms and environmental variables often do not hold up over time due to an ephemerality of relationships between the two types of variables (DeYoung *et al.* 2004b). For example, relationships between two variables may only exist during certain times of the year, or only when certain levels of each variable exist. Both variables may also be affected by other related variables which might alter the original relationship, causing it to disappear. These sorts of relationships are easy to visualize in systems as complex and fluid as the ocean.

Summer gray whale abundance off the west coast of Flores Island, British Columbia (BC) (Figure 2), varies on an annual basis. These variations have led to questions regarding the reasons behind these fluctuations, and the effect of oceanographic and environmental forcing variables on gray whale abundance experienced through the food web. Environmental variables such as SST, salinity, wind speed, upwelling and sunlight all have the potential to influence the quantity of prey available to foraging gray whales, and thus also influence the abundance of gray whales.

Gray whales and gray whale prey

Gray whales migrate annually between the breeding lagoons of Baja California and feeding grounds in the Bering and Chukchi Seas. Some whales do not complete the entire migration to the feeding grounds, but rather stop off at a point along the migration route, such as Clayoquot Sound on the west coast of Vancouver Island, to forage (Murison *et al.* 1984, Duffus 1996, Dunham & Duffus 2001, Calambokidis *et al.* 2002). This use of areas other than the Bering and Chukchi Seas led to the division of gray whale foraging areas into

primary, secondary and tertiary areas depending on the number of whales foraging there (Kim & Oliver 1989). Clayoquot Sound is part of the tertiary foraging area stretching from south-western Alaska to Baja California (Kim & Oliver 1989). Between all foraging areas, gray whales are known to take many types of prey (Nerini 1984, Kim & Oliver 1989), exhibiting a foraging plasticity which allows them to take advantage of the most abundant food source available.

Foraging gray whales are concentrated in Clayoquot Sound between June and September, although some individuals have been observed to arrive earlier and/or stay longer. Several types of foraging habitat may be used depending on the prey species, including sandy areas, open water , mud flats and rocky piles or kelp beds (Dunham & Duffus 2001), thus demonstrating the aforementioned plasticity in foraging behaviour even over a relatively fine spatial scale such as several kilometres. The primary prey items of gray whales in these areas are amphipods, crab larvae, ghost shrimp and mysids (Dunham & Duffus 2001). The main prey items of gray whales foraging near the coast of Flores Island are mysids (Family Mysidacea), small 'opossum shrimp', that congregate in patchy hyperbenthic swarms (Clutter 1969) over rock piles and in areas where kelp is abundant (Dunham & Duffus 2001, Dunham & Duffus 2002, Patterson 2004); some species have been observed to live in the kelp itself (Turpen *et al.* 1994). Nine species of mysids have been identified in the study area, with *Holmesimysis sculpta* being the numerically dominant species (Patterson 2004), as has been observed in other areas of the BC coast (Stelle 2001). Little information is available on the specific life history or foraging habits of the population of mysids in the study area and of the species of mysids in general, making the attempt to connect environmental variables with gray whale abundance more difficult, since the time scales over which energy is transferred between levels of the food web are currently unknown.

The effects of gray whale foraging on future gray whale abundance are also unknown; that is to say it is unknown whether long-term prey abundance is affected by or related to gray whale foraging bouts. Top-down pressures are important in regulating populations of organisms through predation, but their effects in an environment such as the ocean, where both predators and prey are distributed in a patchy manner, particularly in terms of whales and their prey (Croll *et al.* 1998), is unknown for gray whales. However, it can be

assumed that predation must have some effect on some scale, or that the abundance of gray whales in adjacent time periods should be related, although a relationship may or may not exist at the scales examined in this research.

Modeling gray whale abundance – objectives of this study

Modeling the relationships between physical oceanography and organisms higher up the food web, such as zooplankton and fish, has been described as being very complex and difficult (DeYoung *et al.* 2004b). Studies such as this one although not simple to undertake, are necessary to fill the gaps between environmental parameters and measurable gray whale abundance in order to expand our knowledge of the effects of environmental variables on upper trophic level predators. Relating environmental variables to variations in gray whale abundance has not been attempted previously, but other studies have linked the distributions or abundance of marine mammals and other high-trophic level predators to environmental forcing factors (Andrade & Garcia 1999, Hare & Mantua 2000, Littaye *et al.* 2004, Croll *et al.* 2005, Keiper *et al.* 2005), allowing the authors to expand on current knowledge regarding general and temporal aspects of energy transfer up the food web and on the variables or phenomena driving the distribution and abundance of marine mammals over time. Some of these studies were located offshore or in deeper waters, so other physical oceanographic variables may be important there, such as thermocline depth, as noted by Keiper *et al.* (2005) and Eslinger *et al.* (2001). Such variables are not as likely to play a role in a very shallow, nearshore environment as the one where foraging gray whales are located and as such are not considered in this study. Few or no studies have examined the relationship between environmental variables and a top predator which forages as close to shore as does the gray whale.

The search for relationships between gray whale abundance and environmental variables is the main focus of this project. In completing this analysis, the temporal scale of potential gray whale responses to environmental forcing is examined by searching for relationships between data aggregated at different time scales. Where possible, time lags will also be identified which will expand the knowledge of the temporal aspect of food web interactions. Statistical relationships between environmental forcing variables at a broad

spatial scale and gray whale abundance at a fine spatial scale will hopefully improve the understanding of the coupling of data at different scales.

Data

Study area

The study area is located between 49º14'N 126º05'W and 49º19'N 126º14'W along the southwest coast of Flores Island, BC, Canada in the traditional territory of the Ahousaht First Nation (Fig. 2).

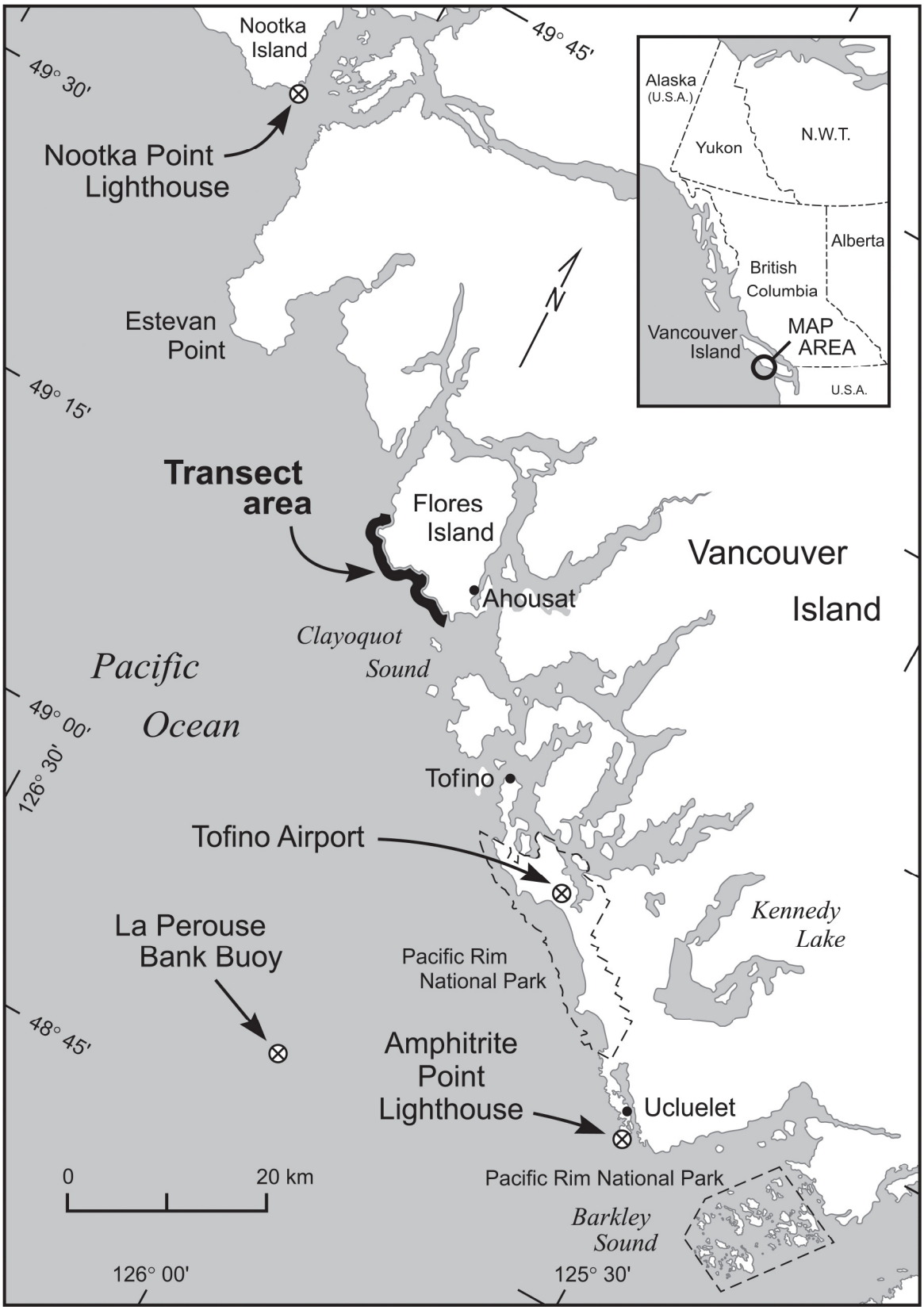


Figure 2. Map of the study area.

The coastline of the area is a rocky shoreline punctuated by a few pebbly or sandy beaches and bays. Substrate types in the area of the transect range from sandy to rocky to sandy with shells. Several species of macroalgae, predominantly bull kelp (*Nereocystis luetkeana*), grow along the majority of the shorelines and in Cow Bay.

Dependent variable - gray whale surveys

The study survey was 12km long and followed the coast of the island at approximately the 10m depth contour (see Fig. 2), as the majority of foraging gray whales were observed within this area. Gray whale surveys were completed between May 15 and September 15 of each year between 1997 and 2004. Surveys were conducted from a 7m research vessel equipped with nautical charts and GPS. Counts of gray whales along each transect were taken by 3-4 researchers and assistants covering 360° around the vessel while one researcher or assistant recorded the data. Observers differentiated between individuals through recognition of differences in skin pigmentation and markings, thus double-counting is unlikely. The surveys were unequally spaced in time and thus each year of gray whale survey data is characterized by a different number of surveys (Table 1).

Year	No. surveys	No. whales	Whales survey^{-1}
1997	54	393	7.28
1998	60	639	10.65
1999	40	158	3.95
2000	31	69	2.23
2001	54	121	2.24
2002	40	488	12.2
2003	31	168	5.42
2004	30	284	9.46

Table 1. Number of whales observed per year and number of surveys per year.

The number of whales and number of surveys were aggregated at four different time scales: weekly, semi-monthly, monthly, and yearly. To address the unequal numbers of surveys per period, the number of surveys and number of whales observed were transformed into a mean value representing the number of whales observed per survey. These data, aggregated at the four different time scales, were tested for normality using Kolmogorov-Smirnov (K-S) tests.

The data were observed to be normally distributed at all four time scales. The data were also plotted in scatterplots against the independent variables to examine the distribution and to search for outliers. The scatterplots revealed that there were no extreme outliers, and that the scatter showed either weak linearity or no other pattern when compared with example distributions such as polynomial distributions.

In terms of other data characteristics, these whale abundance data are considered to be quite reliable, and as such to have low measurement error. This is due to the level of experience of the researchers taking the whale data, and to the fact that whales may be distinguished from one another due to differences in skin pigmentation. As such, the chance of whales being counted multiple times is low. It is possible that some whales evaded being observed during the transects, but this is unlikely due to the slow pace of the research vessel and the large number of researchers observing in all quadrants around the research vessel. To ensure the greatest data reliability, all gray whale data were included in the analyses; that is to say that the data are not sample-selected. The data used for these analyses is continuous between 1997 and 2004.

Independent variables

The independent variables were selected for two reasons: 1) their potential to influence gray whales through the food web; most of the variables act as direct growth stimuli of phytoplankton or kelp, which is assumed to then affect the growth of zooplankton such as mysids, influencing the abundance of gray whale prey, and thus the abundance of gray whales, and 2) the accessibility of the data. Both are appropriate reasons to choose independent variables (Tabachnick & Fidell 1983). I selected the following:

- **Temperature** exerts control on the growth rates of phytoplankton and zooplankton, with warmer temperatures leading to faster growth to a point (Lalli & Parsons 1997, Ishizaka *et al.* 1983); thus measures of SST are an important factor to include in the model.
- **Salinity** affects the buoyancy of phytoplankton and zooplankton (Bienfang & Szyper 1982, Niemi 1982), thus affecting the ability of these organisms to stay in the euphotic layer, and thus influencing their abundance, growth and reproduction rates.

- **Wind speed** affects the amount of mixing of the water column and is related to upwelling or downwelling in coastal areas, depending on wind direction (Thomson 1981).
- **Upwelling** (the process of colder, nutrient-rich water being moved upward in the water column by a combination of coastal winds and Coriolis force) brings nitrates and other nutrients to the surface where they are used by phytoplankton (Lalli & Parsons 1997) and thus is closely related to phytoplankton production.
- **Sunlight** is also an important factor, since phytoplankton and macroalgae are photosynthetic organisms and thus need sunlight for growth, more hours of bright sunlight per day will increase phytoplankton production (to a point) (Duarte 1990, Lalli & Parsons 1997), and in some areas, light is the main trigger for phytoplankton growth (Bleiker & Schanz 1997).

Details of independent variables and their sources are listed in Table 2. The variables selected here to be used as independent variables in this analysis were also selected because they were expected to interact with each other on some level to create a hospitable environment for phytoplankton and zooplankton growth. For example, a larger number of hours of sunlight combined with a greater amount of upwelling in a particular year could be postulated to create good conditions for phytoplankton growth.

Since the study area is located within 1 km of the shore, it should also be receiving a certain amount of runoff and thus sediment and nutrients. No data were available to test river runoff for nutrients, but past research revealed that nutrients were highly retained in the terrestrial system (Karagatzides 2006), theoretically reducing the nutrient input from a main drainage basing to the ocean at Cow Bay. Any nutrient input should vary with hydrological events, and therefore may be important as a nutrient source at certain times of the year. However, as no data are available on nutrient input from terrestrial sources, this issue is not considered in this study.

Variable	Source	Internet Location
Sea surface temperature, Amphitrite Lighthouse	Fisheries and Oceans Canada Lighthouse Database	http://www-sci.pac.dfo-mpo.gc.ca/osap/data/SearchTools/Searchlighthouse_e.htm
Sea surface temperature, Nootka Lighthouse	Fisheries and Oceans Canada Lighthouse Database	http://www-sci.pac.dfo-mpo.gc.ca/osap/data/SearchTools/Searchlighthouse_e.htm
Salinity, Amphitrite Lighthouse	Fisheries and Oceans Canada Lighthouse Database	http://www-sci.pac.dfo-mpo.gc.ca/osap/data/SearchTools/Searchlighthouse_e.htm
Salinity, Nootka Lighthouse	Fisheries and Oceans Canada Lighthouse Database	http://www-sci.pac.dfo-mpo.gc.ca /osap/data/SearchTools/Searchlighthouse_e.htm
Wind speed, La Perouse Bank Buoy	Fisheries and Oceans Canada MEDS database	http://www.meds-sdmm.dfo-mpo.gc.ca/meds/databases/Wave/WAVE_e.htm
Bakun Upwelling Index, calculated for 48ºN	Pacific Fisheries Environmental Laboratory Database	http://www.pfeg.noaa.gov/products /PFEL/modeled/indices/upwelling/NA/data_download.html
Bakun Upwelling Index, calculated for 51ºN	Pacific Fisheries Environmental Laboratory Database	http://www.pfeg.noaa.gov/products /PFEL/modeled/indices/upwelling/NA/data_download.html
Hours of bright sunlight, Tofino Airport	Environment Canada	None

Table 2. Independent variables and data sources.

All data were collected by the respective sources on a daily basis, except wind speed, which was recorded hourly. Data for upwelling indices at two locations (five locations for the yearly analysis) were used to test relatedness between broad scale upwelling and the gray whale abundance in the study area. Salinity and SST data from two different locations were also used for the same reason, and to test whether data from one location offered a stronger relationship than another. Daily values of SST, sea-surface salinity (hereafter referred to as salinity), sunlight, and Bakun Upwelling Index – hereafter referred to as upwelling – were analysed for missing data and errors. No errors were discovered in the SST, salinity and upwelling data, but missing value tags inserted by the data collection agencies were deleted to avoid altering the analysis. The wind speed data were more problematic and required a different approach. There were several time periods in the data where it appeared that the buoy malfunctioned, recording for example three successive weeks of 0 ms^{-1} wind speed

during January, an extremely unlikely event. Thus, a rule was created where data for any continuous >2 week period during the winter with wind speed values between 0 and 1 ms^{-1} were removed from the data set.

After any errors or missing data tags were removed, the data were converted into mean values on weekly, semi-monthly, monthly, and annual temporal scales. Each mean was constructed separately, so that the temporal scales can be compared (i.e. none is a mean of means). Wind speed data were examined and the maximum speed was extracted for each day, then the daily maximum wind speeds were averaged to produce weekly, semi-monthly, monthly, and annual mean values.

Methods

For this study, the method chosen was regression analysis, which allows for the exploration of cause and effect between independent and dependent variables. Other analyses that also explore relationships between variables, such as correlation analysis, are also useful for estimating dependent variables based on changes in independent variables.

Correlation analysis is a useful statistical tool to use to investigate relationships between variables. Using the calculation of the correlation between two variables believed to be related, *x* and *y*, the object is to show that *y* is a function of *x*. This means that as there are changes observed in values of *x*, there will be corresponding changes observed in the value of *y* (Draper & Smith 1981). However, it is important to note that this relationship, or correlation, does not imply that any type of causal relationship exists between *x* and *y* (Draper & Smith 1981). Such conclusions could be used to improperly illustrate far-fetched situations, for example: that gray whale abundance influences wind speed at La Perouse Bank (which is clearly impossible). Also, correlations provide information on the strength of the relationship between two variables that, while important, is not the central motive for this study.

To achieve the further information needed to imply causality, it is necessary to use regression analysis (Draper & Smith, Milton 1999). Regression uses knowledge of the values of one or more independent variables to estimate or predict values of another (dependent) variable of interest (Milton 1999). Using regression, environmental variable(s) can be considered as the independent variable(s), while the variable of interest, gray whale

abundance, can be considered as the dependent variable. The results from regression analyses will provide information on the contribution of the environmental (independent) variables in predicting or estimating values of gray whale abundance, which is one of the main objectives of this study.

Thus, correlation is a useful tool, in that it can be used to assess the strength of a relationship between two variables, but it does not imply cause and effect, which were the main interests of this study. Thus, regression analysis was used to investigate whether or not changes in specific independent variables, the environmental variables, were causing changes in the dependent variable, gray whale abundance.

Regression assumptions

In order for regression analysis to be used to assess relationships between variables, there are several assumptions which must be met. The main assumptions are: all data exhibit normal distributions, the data show linear pattern when plotted in a scatterplot, all offending outliers have been identified and/or removed, and independence of data points from one another (lack of temporal autocorrelation). It is also important to consider the number of observations and the number of variables necessary for a statistically sound analysis. These assumptions are drawn from several statistical texts, including Tabachnick and Fidell (1983), Draper and Smith (1998), Hair *et al.* (1998), Milton (1999) and Mickey *et al.* (2004).

- **Normality:** The assumption of normality is important to address to ensure that data are not distributed in an unusual trend (positive or negative skewness). To test for univariate normality, I conducted Kolmogorov –Smirnov (K-S) tests on all variables at all temporal scales (Appendix II).
- **Temporal autocorrelation**: Data used in regression analyses must also be temporally uncorrelated (Draper & Smith 1998). To identify temporal autocorrelation, I used the Durbin Watson statistic for all multiple regressions, evaluating whether or autocorrelation was present, and if it was, whether it was negative or positive. Values for the Durbin-Watson statistic range from 0-4, with 0 indicating extreme positive autocorrelation and 4 indicating extreme negative autocorrelation (Draper & Smith 1998). Thus, a value of 2 is considered to exhibit no autocorrelation I used the range

of 1.5 to 2.5 to indicate low autocorrelation of either direction; values above and below that range were identified as exhibiting autocorrelation.

- **Multicollinearity**: Multicollinearity occurs when two or more independent variables affect the dependent variable in the same manner. To identify multicollinearity, I used the variance inflation factor (VIF). This measure shows to what extent each independent variable is explained by other independent variables, thus showing those which are too similar, and would affect the dependent in a similar manner. Hair *et al.* (1998) identify VIF values above 10 any particular variable as being multicollinear with the other variables. In this analysis, I inspected all multiple regression VIFs for multicollinearity. In the analyses presented in this study, it was especially important to pay attention to correlation between independent variables, since many are related to each other. For example, the magnitude of upwelling is influenced by wind speed, and upwelling in turn influences both salinity and SST. Thus, the VIF values were very carefully inspected for any signs of multicollinearity. To address issues of spatial autocorrelation, I did not combine variables measuring the same environmental measure, such as SST, in the same analyses.
- **Linearity:** If a non-linear relationship is assessed with linear regression, only the linear components of the relationship will be considered in the analysis, and the full extent of relationships between the variables may not be understood by the researcher (Tabachnick & Fidell 1983). Linearity was assessed here by using bivariate scatterplots as recommended by Tabachnick and Fidell (1983) and Milton (1999). Although the scatterplots created for this analysis do not necessarily show linearity, they show general scatter or minimal linearity, and they do not show other distributions such as asymptotic or cubic, which would indicate that another analysis method would be more appropriate (see Appendix I for the results of all scatterplots).
- **Outliers:** Scatterplots at all scales were visually inspected for outliers, although in most cases, especially at shorter time scales, the scatter was so great that there would have been little use removing one or two slight outliers; there was no relationship visible in the data to speak of, and thus it would have made no difference to the results.

- **N:** The number of observations (N) to be regressed is also an important consideration. Tabachnick and Fidell (1983) state that in the case of regular regression, it is ideal to have 20 times more cases than variables. Since the current study is considered to be exploratory, the requirements for sample size are not met at every time scale, particularly the annual scale, where N = 6-8 and the number of variables = 2. The analysis was carried out on the full series of data available, so in this case there is simply no more data to be had at this point in time. However, it is important to remember the ramifications of reduced sample size when interpreting the results of the regression analyses; they cannot be infallible.

Single regressions

Single regressions were carried out on all independent variables aggregated at four different time scales; weekly, semi-monthly, monthly and annually, with whales per survey as the dependent variable. The effect of year and time scale (i.e. month, semi-month and week) were also tested to help identify any years or periods significantly different from the rest, which may highlight particular environmental events occurring in that year or period. These 'time' regressions are simple tests of whether there is a relationship between any particular time period and the number of whales per survey in that same period. To test for the presence of time lags, each independent variable was lagged at one, two and three periods and one year for all regressions at all time scales. The annually aggregated data were only lagged two periods due to a short data series and the resultant small number of observations.

Multiple regressions

The two following criteria were created that variables had to meet to be included in the multiple regression models: 1) they had to explain at least 10% of the variance in the single regressions (rounded), and 2) they had to be significant at p=0.1; while this may seem to be a rather high p-value, it was designed only to create a rough criteria by which variables could be evaluated. Variables adhering to these criteria were then entered into a multiple regression model. The multiple models were evaluated more stringently in terms of p-values and the amount of explanation of the variance that each variable returned after regression.

To create a credible model with multiple predictor variables, it was necessary for the combination of multiple variables to explain the most variance possible; models explaining less than 40% of the variance, or models not significant at the 0.1 level were not considered to be useful.

Multiple regressions were carried out on all independent variables aggregated at the same four time scales, weekly, semi-monthly, monthly and annually. In the interest of investigation, all possible combinations of independent variables were entered into multiple models in order to assess the effects of all variables combined with one another. Theory directed the choices of independent variables, but the time scales and pathways of effects on the dependent are not always clear, and thus an investigative approach is warranted here.

To address the issues of multicollinearity and autocorrelation, VIF values were inspected for multicollinearity (values greater than 10) and Durbin-Watson (D-W) values were inspected for serial autocorrelation (values less than 1.5 or greater than 2.5). Multiple regression models were evaluated for the number of variables they used in comparison to the amount of variance explained by these variables.

Results

Results are presented in the order of analysis, with single regressions presented first followed by expansion on the results organised by independent variable and multiple regressions presented second followed by a review of the results of the models organised by time scale. Only significant results ($p<0.1$) are presented here (see Appendix III for results of all models).

Table 3 lists regressions preformed at a weekly time scale, Table 4 lists regressions performed at a semi-monthly time scale, Table 5 lists regressions performed at a monthly time scale and Table 6 list regressions performed at an annual scale. The variable column identifies the independent variables used in the regression analysis; the dependent variable is always whales per survey, aggregated to the time scale of the regression being performed. The R^2 column represents the R^2 value of the regression and the 'p' column lists the significance of each regression.

Single regressions

Variable	R^2	p
SST - Nootka	0.097	0.001
Whales per survey - lagged 1 week	0.630	0.000

Table 3. Single regressions – weekly temporal scale. Independent variables are listed in the 'Variables' column; the R^2 column represents the R^2 value of the regression and the 'p' column lists the significance of each regression.

Variable	R^2	p
SST - Amphitrite	0.118	0.006
SST - Nootka	0.161	0.001
Wind speed - La Perouse Bank - lagged 3 periods	0.104	0.009
Whales per survey - lagged 1 period	0.512	0.000

Table 4. Single regressions – semi-monthly temporal scale. Independent variables are listed in the 'Variables' column; the R^2 column represents the R^2 value of the regression and the 'p' column lists the significance of each regression.

Variable	R^2	p
SST - Amphitrite	0.147	0.021
SST - Nootka	0.197	0.007
Salinity - Nootka	0.100	0.061
Wind speed - La Perouse Bank - lagged 2 months	0.141	0.024
Sunlight - Tofino	0.118	0.041
Sunlight – Tofino - lagged 12 months	0.104	0.055
Whales per survey - lagged 1 month	0.105	0.092
Month = July	0.166	0.014

Table 5. Single regressions – monthly temporal scale. Independent variables are listed in the 'Variables' column; the R^2 column represents the R^2 value of the regression and the 'p' column lists the significance of each regression.

Variable	R^2	p
Wind speed - La Perouse Bank	0.646	0.016
Upwelling- 48°N - lagged 2 years	0.457	0.066
Upwelling - 45°N - lagged 2 years	0.552	0.035
Upwelling - 54°N	0.633	0.018

Table 6. Single regressions – yearly temporal scale. Independent variables are listed in the 'Variables' column; the R^2 column represents the R^2 value of the regression and the 'p' column lists the significance of each regression.

Gray whale abundance and SST

The R^2 values for SST were low at the monthly, semi-monthly, and weekly time scales, and only two time scales were significant; monthly (Nootka: $R^2 = 0.197$, $p = 0.007$; Amphitrite $R^2 = 0.147$, $p = 0.021$) and semimonthly (Nootka: $R^2 = 0.097$, $p = 0.001$). This shows that of the temporal scales tested here, the temporal scale over which SST is best related to the number of whales per survey ranges between two weeks and one month. Of course, some relationship may also exist at a scale between one month and one year or over one year, but that was not tested in this analysis.

Broad scale SST regimes have the ability to affect fine scale biological processes. Although SST at Nootka explains only ~20% of the variance, this is still a large amount to be explained by a single variable. The correlation between the number of whales per survey and SST is positive, indicating that as temperature increases, the number of whales per survey also increases. This follows the general rule that as temperature increases, phytoplankton growth also increases (to a point) (Lalli & Parsons 1997, Ishizaka *et al.* 1983), theoretically resulting in greater prey for zooplankton, greater zooplankton production, and greater abundance of gray whales feeding on the increased zooplankton.

Gray whale abundance and salinity

The results of these analyses indicate that salinity generally does not play a role in determining gray whale abundance for these data, as R^2 values were low at all four temporal scales. Salinity was only significant at one time scale, the monthly scale (Nootka: $R^2 = 0.100$, $p = 0.061$). The correlation between salinity at Nootka and the number of whales per survey is positive, indicating that as salinity increases, gray whale abundance increases. This may be related to the increased buoyancy of phytoplankton in higher salinity/higher density waters, which would in turn reduce phytoplankton losses to sinking. Salinity may not have been significant at the yearly time scale due to an overall homogeneity of annual salinity values.

Gray whale abundance and wind speed

Wind speed is an important variable in that it has the potential to determine the distribution of organisms and nutrients through influencing such processes as upwelling or by

disturbance/mixing of the water column. R^2 values were significant but offered low explanatory power at semi-monthly and monthly scales (wind speed lagged 3 semi-monthly periods: $R^2 = 0.104$, $p = 0.009$; wind speed lagged 2 months: $R^2 = 0.141$, $p = 0.024$). However at an annual scale, a much larger amount of the variance is explained ($R^2 = 0.646$, $p = 0.016$), with no lags (see Fig. 3 below). Residual plots show good scatter, as desired. These results indicate that wind speed is likely an influence at time scales from six weeks to two months to one year, with the amount of variance explained increasing as the length of time period increases. Wind speed aggregated over a longer period of time is more likely to be explanatory because it is highly variable in the short term, and averaging data over the long-term should reduce this variability. The correlation between wind speed and whales per survey is negative, indicating that as wind speed decreases, the number of whales per survey increases.

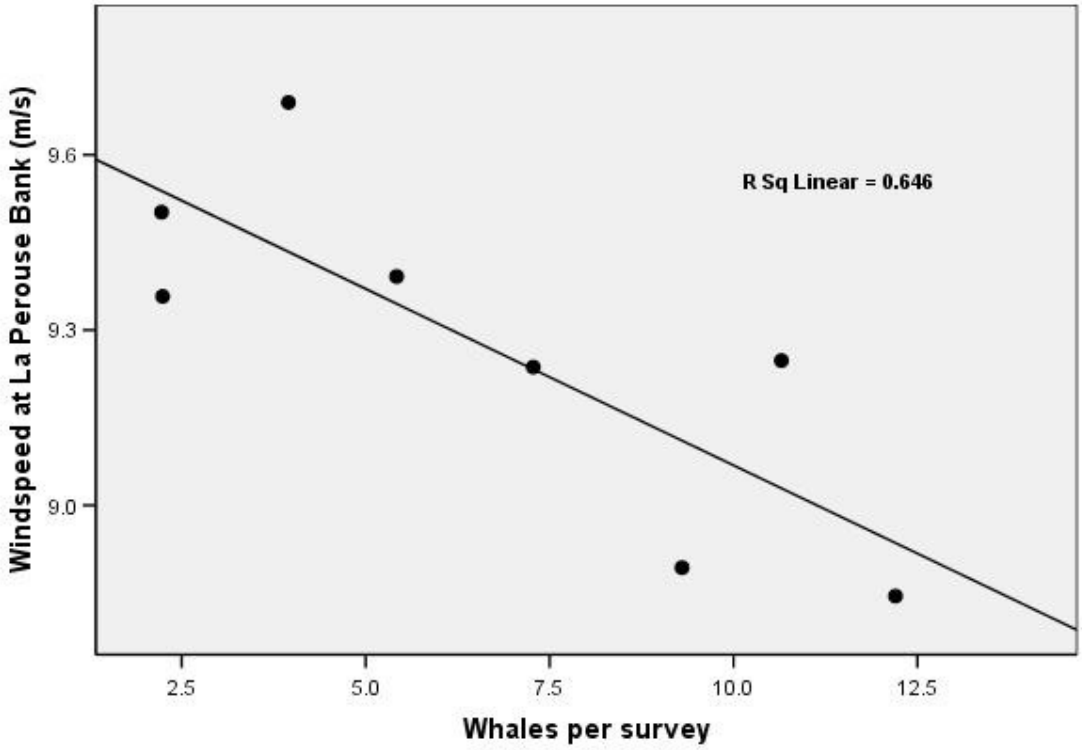


Figure 3. Scatterplot of whales per survey and wind speed at La Perouse Bank at an annual time scale. Line represents a linear fit line, and R Sq Linear represents the R^2 value of the regression.

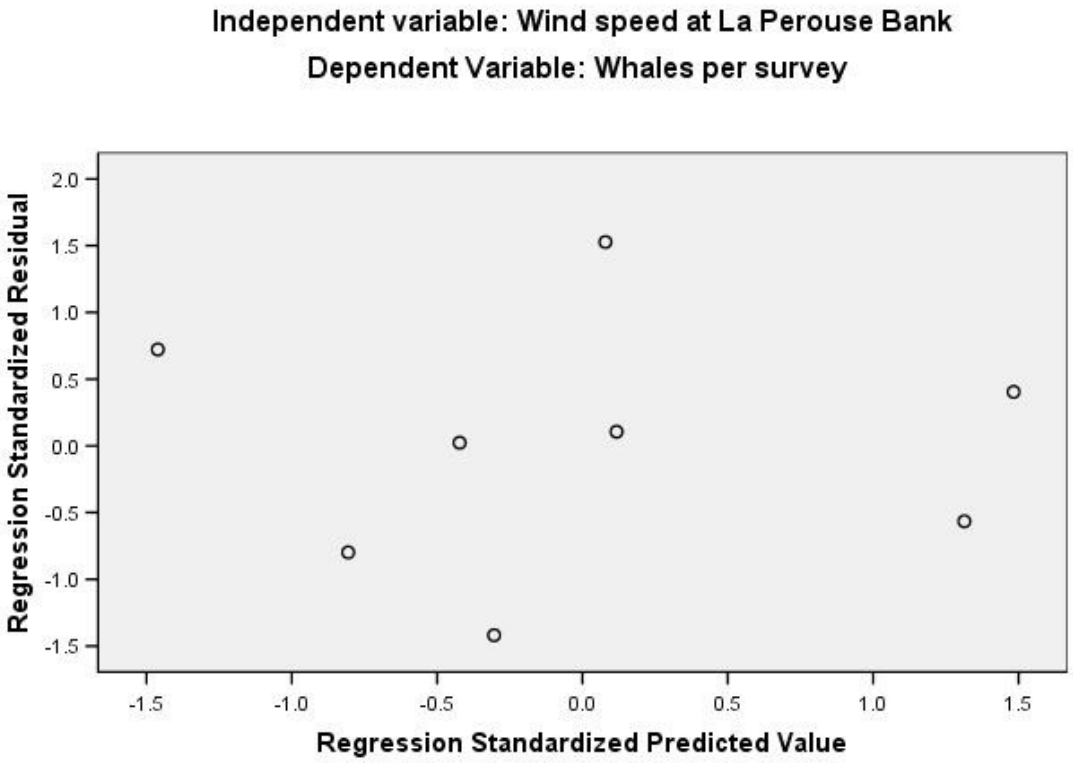


Figure 4. Residuals for single regression: whales per survey and wind speed at La Perouse Bank, at an annual time scale.

Gray whale abundance and upwelling index

Upwelling was expected to play a major role in influencing gray whale abundance through the supply of nutrients to the local food chain at several different time scales; however, this was not observed in the analyses conducted here did not reveal many relationships. The only scale at which the upwelling index was related to gray whale abundance was the annual scale. At the annual scale, upwelling lagged 2 years at 48ºN was related to gray whale abundance ($R^2 = 0.457$, $p = 0.066$; see Fig. 5 below). Residuals showed some scatter (see Figure 6). Interestingly, tests of annual upwelling north and south of the study area also provided results with some explanatory power. These other locations were

only tested at an annual scale, since the analysis indicated that upwelling was only significant at an annual scale. To the north and south of the study area, upwelling at 54ºN was related to gray whale abundance ($R^2 = 0.633$, $p = 0.018$), as was upwelling lagged 2 years at 45ºN ($R^2 = 0.552$, $p = 0.035$). It is interesting that upwelling in the current year at 54ºN explained 63.3% of the variance – no other location or time scale of upwelling data exhibited a relationship with whale abundance in the same year (variables for data at 48ºN and 45ºN were both explanatory at a lag of two years. It is not clear how upwelling measured at 54ºN, 6º north of the study area, would directly affect gray whale abundance in the study area, and thus it is uncertain whether this is indicative of an spurious relationship or simply a complex relationship.

The correlation between lagged upwelling indices and gray whale abundance was positive, indicating that, as predicted, as upwelling increases, the amount of nutrients should also increase, leading in theory to greater phytoplankton production, thus to greater zooplankton abundance and to greater numbers of gray whales.

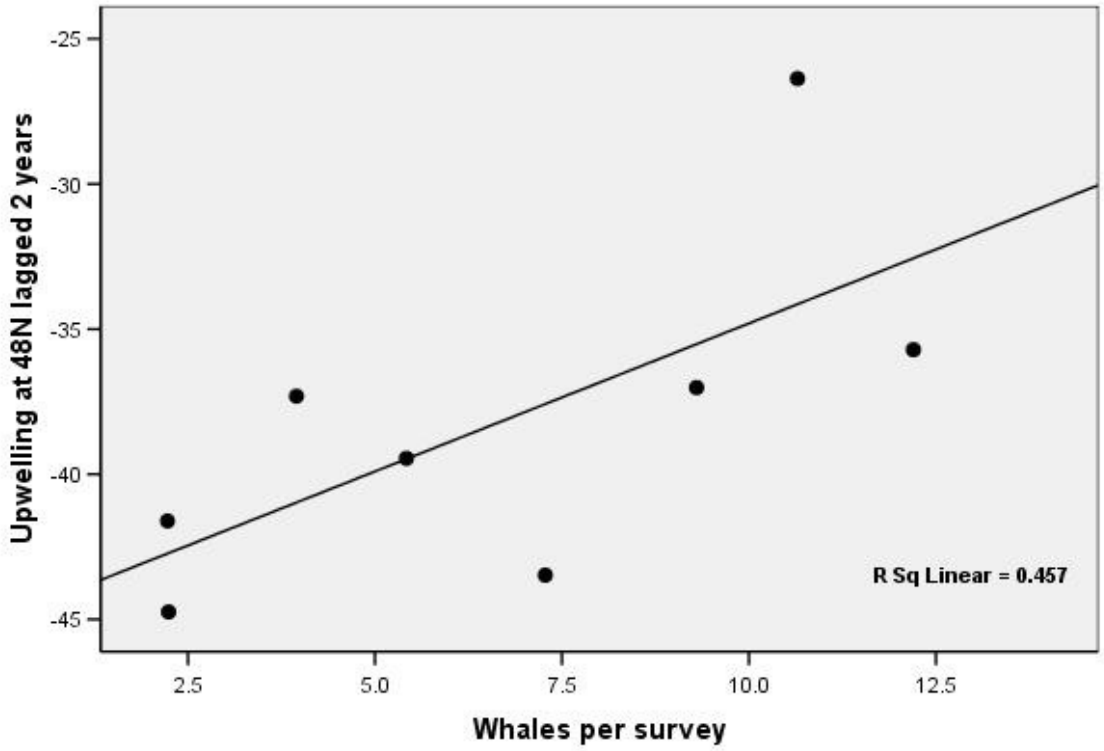


Figure 5. Scatterplot of whales per survey and upwelling at 48°N lagged 2 years, at an annual time scale. Line represents a linear fit line, and R Sq Linear represents the R^2 value of the regression.

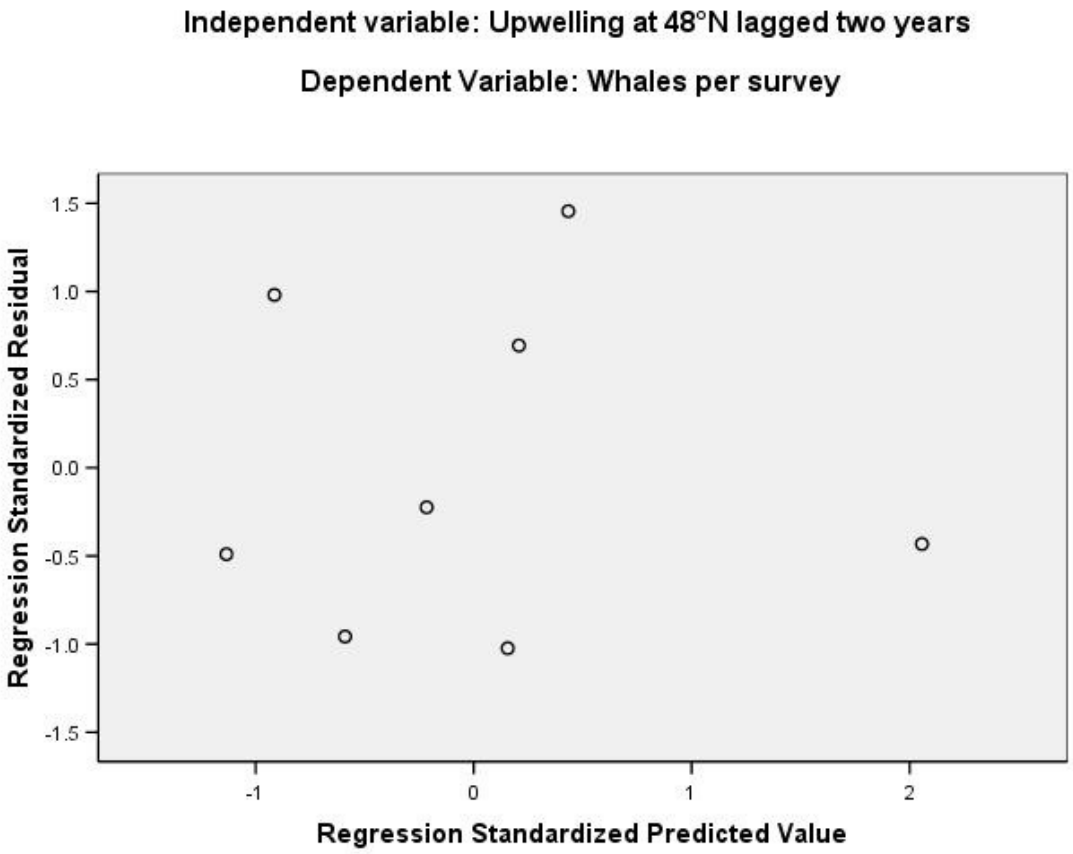


Figure 6. Residuals for single regression: whales per survey and upwelling at 48ºN lagged 2 years, at an annual time scale.

Gray whale abundance and sunlight

The analyses revealed that the sunlight data were only related to gray whale abundance at the monthly scale, where both the same month's sunlight and sunlight lagged 12 months were significant. The explanatory power provided by these two variables was low; sunlight: $R^2 = 0.118$, $p = 0.041$; sunlight lagged 12 months: $R^2 = 0.104$, $p = 0.055$. The correlation between sunlight and whale abundance was positive, as expected; greater amounts of sunlight are expected to result in greater amounts of phytoplankton, greater numbers of zooplankton, and thus greater numbers of gray whales.

Effect of year and time period

Time period and year were tested for each time scale. No significant correlations were observed other than at the monthly scale. At the monthly scale, the month of July contributed a certain amount of explanation of the variance in gray whale abundance (R^2 = 0.166, p = 0.014). This indicates that some event is occurring in July which affects gray whale abundance. However, since the 'month' variable is a dummy variable, it does not identify which factor is causing such an effect and via which mechanisms it is occurring. Thus it is possible to say that the results indicate that an event occurring in July involving a variable untested in this study explains 16.6% of the variance in gray whale abundance, when data are aggregated at a monthly scale. It is also important to note that this is not entirely unexpected since July was noted to be a slight occasional outlier in some years for several variables.

A lack of significant relationships between gray whale abundance and time periods indicates that overall, no time period or year is more important than any other in terms of gray whale abundance. Although gray whale abundance does vary between surveys, the analysis indicates that overall, time period is relatively unimportant in determining the number of whales per survey.

Effect of previous whale abundance/top-down pressures

The relationship between current gray whale abundance and abundance during previous time periods was strongest at short time scales, and diminished to no relationship as time scale lengthened (whales per survey lagged 1 week: R^2 = 0.630, p = 0.000; whales per survey lagged 1 semi-monthly period: R^2 = 0.512, p = 0.00l; whales per survey lagged 1 month: R^2 = 0.105, p = 0.092; whales per survey lagged 1 year: R^2 = 0.022, p = 0.780). The correlation between whales per survey and lagged whales per survey was positive in all cases, indicating no effect of previous gray whale foraging bouts, which was unexpected, given that this demonstrates no effect of prey resource depletion. Top-down effects of foraging gray whales were expected especially in years of high gray whale abundance.

Multiple regressions

Multiple regression results are presented below. Each figure represents a different time scale. The variable column represents the independent variables which were regressed on the dependent variable, whales per survey. The R^2 column represents the R^2 value of the regression and the p column lists the significance. The DW column shows the Durbin-Watson statistic, while the VIF column shows the variance inflation factor. The first figure represents multiple regressions run on data aggregated at a semi-monthly time scale, while the second figures is those at a monthly time scale and the third figure is at an annual time scale. Multiple regressions by week were not possible, as only one environmental variable was significant at the 0.1 level and explained ≥10% of the variance (SST Nootka: R^2=0.097, p=0.001), resulting in no possible combinations for multiple regression analyses.

Variables	R^2	p	DW	VIF
SST – Amphitrite Wind speed – La Perouse lagged 3 periods	0.162	0.005	0.816	1.154 1.154
SST – Nootka Wind speed – La Perouse lagged 3 periods	0.192	0.002	0.840	1.195 1.195

Table 7. Multiple regressions – semi-monthly temporal scale. Independent variables are listed in the 'Variables' column; the R^2 column represents the R^2 value of the regression and the 'p' column lists the significance of each regression.

Variables	R^2	p	DW	VIF
SST – Nootka Salinity – Nootka	0.215	0.018	1.654	1.245 1.245
SST – Nootka Wind speed – La Perouse, lagged 2 months	0.206	0.022	1.581	1.924 1.924
SST – Nootka Sunlight – Tofino	0.275	0.005	1.638	1.024 1.024
SST – Nootka Sunlight – Tofino, lagged 12 months	0.243	0.010	1.546	1.072 1.072
SST – Nootka Salinity – Nootka Wind speed – La Perouse, lagged 2 months	0.222	0.043	1.657	2.114 1.250 1.931

SST – Nootka Wind speed – La Perouse, lagged 2 months Sunlight – Tofino	0.295	0.010	1.678	2.025 1.979 1.053
SST – Nootka Sunlight – Tofino Sunlight – Tofino, lagged 12 months	0.307	0.008	1.564	1.086 1.042 1.092
SST – Nootka Salinity – Nootka Wind speed – La Perouse, lagged 2 months Sunlight – Tofino	0.296	0.024	1.694	2.144 1.440 2.012 1.213
SST – Nootka Wind speed – La Perouse, lagged 2 months Sunlight – Tofino Sunlight – Tofino, lagged 12 months	0.331	0.012	1.625	2.129 1.989 1.069 1.097
SST – Nootka Salinity – Nootka Wind speed – La Perouse, lagged 2 months Sunlight Tofino Sunlight – Tofino, lagged 12 months	0.335	0.025	1.689	2.213 1.517 2.016 1.262 1.156
SST – Nootka Wind speed – La Perouse, lagged 2 months Sunlight – Tofino Sunlight – Tofino, lagged 12 months Month = July	0.374	0.012	1.532	2.167 1.995 1.133 1.215 1.277

Table 8. Multiple regressions – monthly temporal scale. Independent variables are listed in the 'Variables' column; the R^2 column represents the R^2 value of the regression and the 'p' column lists the significance of each regression.

Variables	**R^2**	**p**	**DW**	**VIF**
SST – Nootka Wind speed – La Perouse	0.653	0.071	1.662	1.750 1.750
SST – Nootka Upwelling – 48°N, lagged 2 years	0.630	0.084	2.159	1.091 1.091
SST – Nootka Wind speed – La Perouse Lag 2 upwelling 48°N	0.896	0.020	1.683	1.758 1.810 1.095
Wind speed – La Perouse Upwelling – 48°N, lagged 2 years	0.896	0.004	1.690	1.059 1.059

Table 9. Multiple regressions – yearly temporal scale. Independent variables are listed in the 'Variables' column; the R^2 column represents the R^2 value of the regression and the 'p' column lists the significance of each regression.

Multiple models

Although the four temporally-aggregated data sets with multiple variables were tested for relationships, with explanatory and significant single regression variables used to construct multiple models, only three temporal scales (semi-monthly, monthly and annually) produced models of any interest. The amount of variance explained by the multiple models appears to be linked to the time scale at which the variables are regressed, with models using data aggregated at longer time scales explaining progressively more of the variance than those at shorter time scales.

The semi-monthly scale offered little in terms of explanatory multi-variable models. At the semi-monthly scale, the only two possible combinations of variables were possible, SST at Amphitrite with wind speed lagged 3 semi-monthly periods, and SST at Nootka with wind speed lagged 3 semi-monthly periods. The best model was composed of SST at Nootka and wind speed at La Perouse lagged 3 periods, which explained 19.2% of the variance. The two SST variables were not combined in a multiple regression due to expected high levels of multicollinearity. Multicollinearity was low in the two multiple regressions, with the VIF never surpassing 2, and thus much lower than the cut-off value of 10. Strong positive autocorrelation was identified in the data through Durbin-Watson values of 0.816 and 0.840 for the two models, indicating that correction would have been necessary, had the model been highly explanatory.

At the monthly scale, the greatest number of variables were significant in the single regressions, and were thus available to be used in multiple regressions. However, this did not translate to the greatest amount of variance explained between the three time scales; in fact, multiple models at the monthly scale explained the second highest amount of variance in whale abundance. With so many variables significant in the single regressions, many combinations were possible, and as this is an exploratory study, all possible combinations were tested. The most explanatory model was comprised of SST at Nootka, wind speed at La Perouse lagged 2 months, sunlight at Tofino, and sunlight at Tofino lagged 12 months; it explained 37.4% of the variance. This model is the most useful of all the monthly models tested in terms of explaining the variance, but in an overall sense, the variance explained is still low, at less than 40%. Multicollinearity was not observed to be a problem in the monthly analyses, with all VIF values falling below 3, well below the cut-off of 10. All

Durbin-Watson values for the monthly models were above the cut-off of 1.5, signifying no or low autocorrelation, although most were close to this cut-off value.

The yearly scale offered the most useful multiple models in terms of explanatory power. Only two environmental variables were selected from the single regressions at the yearly scale; upwelling at 48ºN lagged 2 years and wind speed at La Perouse. Even alone, these variables explained a greater amount of the variance than the best monthly model. Although SST at Nootka was not significant at the yearly scale, it was added to the multiple regressions out of curiosity; it added only a small amount of explanatory power when combined with wind speed, slightly more to upwelling, and none at all to a model of wind speed and upwelling, so it was removed in the final model. All Durbin-Watson statistics were between the cut-off values for the yearly models, indicating low or no autocorrelation. All VIF values for this model were near 1 and thus well below the cut-off of 10. Thus, the yearly model comprised of wind speed at La Perouse and upwelling at 48ºN lagged 2 years explaining 89.6% of the variance offers the best overall model at all of the scales tested in this study, and will from here forward be referred to as the best model.

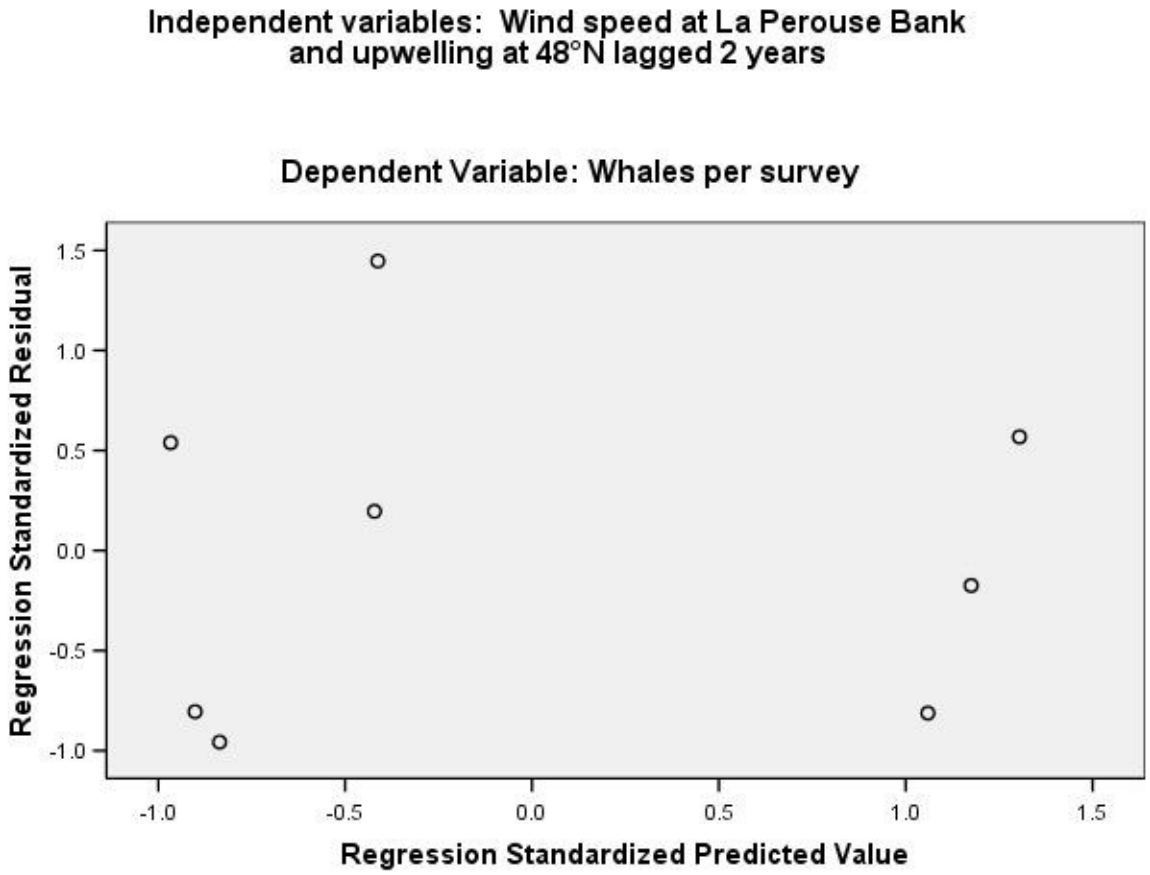


Figure 7. Residuals for the best multivariate model: whales per survey as dependent variable; upwelling at 48ºN lagged 2 years and wind speed at La Perouse Bank as independent variables.

In the hopes of relating gray whale abundance in the study area to productivity north and south of the study area, extra variables were added to test upwelling at 42ºN, 45ºN and 54ºN. These were tested in single regressions at a yearly scale. The only results which were significant were upwelling at 54ºN (north of the study area) which explained 63.3% of the variance, and upwelling 45ºN lagged 2 years (south of the study area) which explained 55.2% of the variance. When added to the multiple regressions, these variables added no explanatory value to the two main variables already in use. However, it is important to note their significance in relation to gray whale abundance. The positive relationship between upwelling at 45ºN lagged 2 years and whales per survey is the same as for upwelling at 48ºN lagged 2 years, indicating that the region of 45ºN is related in the same way as 48ºN to whales per survey, possibly indicating spatial homogeneity or a regional effect. Upwelling at

54ºN, however, was only significant at the current time period, and not at a lag, indicating that this area's upwelling has a different relationship with gray whale abundance in the study area, and thus is not homogeneous with areas to the south, including 48ºN and 45ºN.

Although the yearly multiple best model is highly explanatory, explaining 89.6% of the variance, it is still important to note that there are some drawbacks to using this yearly data. The main issue with the use of these data is the very small number of observations (N = 6-8). With so few observations, it is more likely that the regression analysis can be affected by any one point. This can be particularly problematic if there are any outliers, the lack of which is also a main regression analysis assumption (see *Regression Assumptions* above). To test the effect of each observation on the regression results, the observation for each year was removed from the original dataset, then the regressions were run again. This was done for the regressions of the significant single variables; wind speed at La Perouse Bank and upwelling at 48ºN lagged 2 years, and for the multiple model created with those two variables. The R^2 value changed somewhat with the range between minimum and maximum R^2 values being 0.274 for wind speed at La Perouse, and 0.230 for upwelling at 48ºN lagged 2 years. These changes in R^2 values reveal that the regression equation works better or worse in different years. In other words, each variable is not affecting the number of whales per survey to exactly the same extent in each year. However, the R^2 values of the multiple model changed even less, with the range in R^2 values being 0.124. These results show that although the data did not contribute to the regression results with precisely the same effect in each year, this did not highly affect the usefulness and accuracy of the multiple model results, and thus no year is such a strong outlier that it should be removed from the analysis.

Challenges to data analysis

In this study, environmental variables are utilised in regression analyses to investigate the relationship between environmental forcing factors and gray whale abundance. There are several conditions which must be met in order to complete valid regression analyses; these conditions are discussed in detail below.

Gray whale abundance was collected along a transect designed to sample gray whale foraging areas. The main challenge to using transect data is spatial autocorrelation, or that the gray whales were not randomly sampled; rather the presence of each whale was related to

the presence of other whales, as they were all in the area for the purpose of feeding. Thus, no one gray whale observation is independent from another. Spatial autocorrelation is not necessarily a negative aspect of data; it can be used to assess the relatedness of two or more samples, and is useful in determines the spatial scale of patches of organisms, such as to assess the dimensions and relatedness of patches of zooplankton (Natunewicz & Epifanio 2001), and how zooplankton patch dynamics vary by species (Curtis 2004). Spatial autocorrelation is inherent in the type of data used in this study, that being data collected along a transect. However, since the concentration of gray whales in the study area was in fact the reason behind which sampling was taking place; this is deemed acceptable in terms of analyzing such data (Legendre & Legendre 1998), as it is in this study.

Other than spatial autocorrelation, there are also another few specific statistical challenges to address prior to running the regression analyses. There are two main problems which may arise when analysing data in a continuous series with variables which are related to each other, as the variables in this analysis are. The first main issue is multicollinearity, the second is temporal autocorrelation.

Multicollinearity between independent variables can create erroneous regression results (Hair *et al.* 1998). Although multicollinearity has no actual effect on the estimated variate itself, it can create problems when two or more independent variables affect the dependent in a similar manner. Even low levels of multicollinearity can affect how the researcher interprets the results in terms of explaining the variance (Hair *et al.* 1998); in other words, it can obscure the role of each variable in the multiple regression analysis. If multicollinearity is observed to be a problem, then the variable considered to be the least explanatory should be deleted from the analysis (Tabachnick & Fidell 1983).

The presence of temporal autocorrelation may also create problems in regression analysis. Temporal autocorrelation is usually present at some level in most continuous time series of data, and is simply the relatedness between temporally consecutive observations in a data series. It is generally more prevalent in time series with short time periods between observations, such as data collected on a daily temporal scale (see for example Gallego *et al.* 1996) due to the greater probability of observations being related to one another if they are closer together in time (Bence 1995). Temporal autocorrelation is relatively well-studied in econometrics, where it is a common occurrence in short series (Bence 1995), but it is rather

neglected as a topic in many biological studies. Treating autocorrelated data as if it were a random sample is not statistically sound and results in 'temporal pseudoreplication' (Hurlbert 1984), and may create several serious problems in data analysis and interpretation including increasing the number of Type I errors, reducing the efficiency of estimation of parameters by the analysis, and making the estimation of the linear regression intercept severely inaccurate (Bence 1995).

A simple way to identify some forms of temporal autocorrelation is through the use of the Durbin-Watson statistic (Draper & Smith 1998). Once autocorrelation has been identified, the researcher may choose to simply note its presence or to attempt to remove the autocorrelation from the data (Bence 1995); researchers may also use two other common methods for dealing with severe temporal autocorrelation: 'pre-whitening' and 'first differencing' (Pyper & Peterman 1998). However, no overall consistent autocorrelated trend was observed in any highly explanatory model in this study, and thus these two methods were not necessary.

As a further side note, DeYoung *et al.* (2004a) note that autocorrelation will also exist in abundance measurements of species which live more than one year, such as gray whales and possibly their prey, potentially creating misleading cross-correlations (DeYoung *et al.* 2004a). In the case of gray whales, some individuals return to the study area year after year, and thus these occurrences will be related. In the case of gray whale prey, their abundance will be autocorrelated on an annual scale as it is assumed that they will remain in much the same area, and thus their abundance will be related year to year as long as they live at least two years.

The analysis method of choice should address the above statistical challenges to data analysis. Regression analysis offers a simple method by which to test for the presence and strength of relationships between variables, while assessing the extent to which the chosen independent or predictor variables explain the variance in the dependent variable. The use of multiple independent variables allows for the creation of models which may be used to predict outcome values of the dependent variable given particular values of the independent variable. It also allows the researcher to address both multicollinearity and temporal autocorrelation through using the VIF calculation and Durbin-Watson statistic respectively.

The above section deals only with the statistical challenges to model building. But what of the challenges of fitting statistics to biological entities or relationships operating at unknown time scales? As pointed out by deYoung *et al.* (2004a), the statistical models created must consider the relevant spatial and temporal scales of the organisms in question. Due to the fact that the time scales over which gray whale prey are affected by environmental variables are unknown, data aggregated at several time scales are used in this analysis in order to search for relevant temporal scales. Environmental data were only available at broad spatial scales, and it is important to note that the spatial scale at which the environmental forcing data were recorded may or may not be appropriate in terms of their influence on gray whale prey. However, since the objectives of this study are exploratory rather than explanatory and part of the exploration is to investigate whether scale coupling is occurring and between which scales, this concern can be set aside for the moment.

Model parsimony

Creating a parsimonious model is one of the great interests and challenges of this study. Model parsimony must be balanced against goodness of fit, and thus models utilising greater numbers of independent variables must be compared to the total amount of variance explained, and that explained by each variable. For the multiple regressions tested here, N=6-8 at the annual scale, the number of independent variables = 2 and the amount of variance explained = 89.6%, while at the monthly scale, N = 16-28, the number of independent variables = 5 and the amount of variance explained is 37.4%. Neither model use a large number of independent variables, but this does not necessarily result in parsimony. Tabachnick and Fidell (1983) state that N should be approximately 20 times the number of independent variables. In this case, the yearly scale has only N = 6-8 observations for independent variables = 2, when there should be a minimum of $N \geq 40$. At the monthly scale, 5 variables are used, so $N \geq 100$ would be the minimum, while the actual number is N = 16-28. This does not mean that the results are not useful, rather it is simply important to note this situation when interpreting the results of the models, and when adding future data and re-running the models. In the case of re-running the models, future observations may

alter the R^2 and the regression equation, and thus the applicability and the performance of the model in terms of prediction of gray whale abundance.

Discussion

The results of the single and multiple regression analyses completed in this study show that it is possible to meet the objectives and research questions set forth at the beginning of this study. The first objective was to investigate the relationships between environmental forcing variables and gray whale abundance, and the related research questions asked what role environmental variables play in influencing the relative abundance of gray whales in these data and whether the environmental variables could be statistically linked to gray whale abundance. These questions/objectives were answered/met in the analyses, which show that in the data examined here, there is a relationship between environmental variables and gray whale abundance, and that it can be described in a statistical manner, using single and multiple regression analyses. The role that environmental variables play in determining gray whale abundance is hypothesised here to be a strong one, given that 89.6% of the variance in gray whale abundance aggregated at a yearly scale was explained by two environmental variables, wind speed at La Perouse Bank and upwelling at 48ºN lagged two years.

These analyses also answer the final objective and research question, which addressed the concept of scale coupling, with broad scale environmental data being statistically related to fine scale gray whale data. The results show that scale coupling is indeed possible, and was achieved with good success in the analyses at an annual time scale. The results also allowed for information regarding the second objective and associated research question, that the study would examine the temporal scale over which gray whales respond to environmental variables, and to test for the presence of time lags at different temporal scales. The analyses conducted tested for time lags at all time scales at which data were aggregated, and they revealed several time lags between the environmental variables and the gray whale abundance. Time lags were observed in the single regressions at the monthly, semi-monthly and yearly time scales. The lagged environmental variable that explained the largest amount of the variance was upwelling at 48ºN lagged two years, with data averaged at an annual scale.

The relationships between variables which were investigated using the multiple regression analyses allow for the estimation of which environmental variables are the most important in affecting gray whale abundance over the time periods tested. The ability to switch between food sources allows both gray whales and gray whale prey, such as mysids, to benefit from which prey is most available, but this ability also makes it difficult to trace the pathways of the food web of which they are a component. If different pathways through the food web occur during the same times of the year due to fluctuations in prey resources, then it may be difficult to accurately model the relationship between gray whales, zooplankton, and lower trophic level organisms. This barrier, combined with a lack of life history and historical abundance data for mysids in the study area led to the need for a different approach in terms of modeling, necessitating the use of environmental variables rather than variables based on the actual prey of gray whales. See Fig. 3 for the steps taken to achieve the results discussed here, including the use of independent variables expected to influence gray whale abundance through the food web.

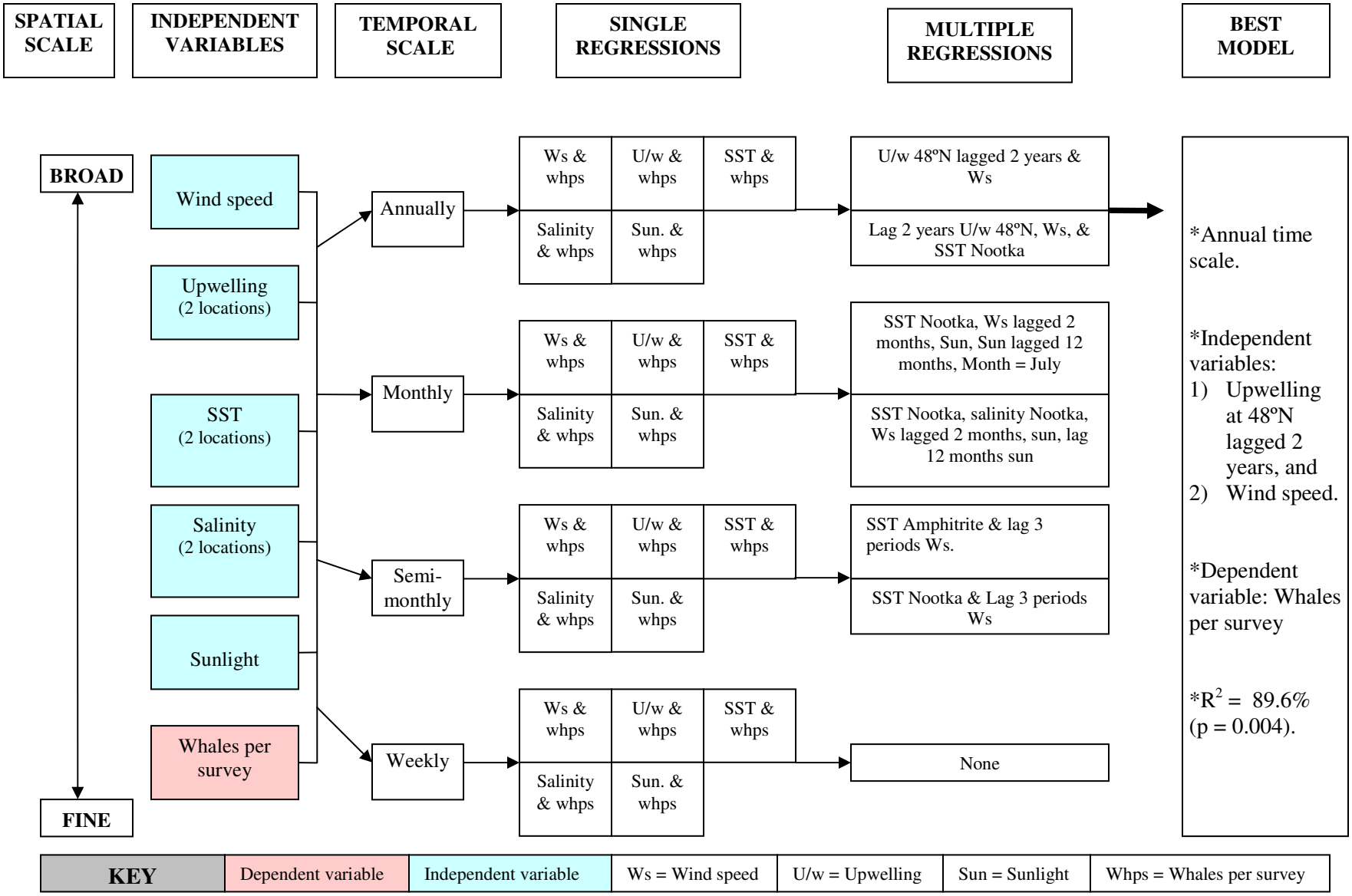


Figure 3. Schematic diagram of steps followed and results obtained during this study.

Model effectiveness and tests of temporal scale

Statistically significant relationships between multiple environmental variables and gray whale abundance were detected at semi-monthly, monthly, and annual scales, although significance varied by temporal scale. The annual scale model explained the most variance in gray whale abundance and is comprised of two variables: wind speed at La Perouse and upwelling at 48ºN lagged two years, which explained 89.6% of the variance ($p=0.004$), and demonstrates the high amount of variance explained at the yearly scale, making it the most effective model of all models tested. Models created at shorter time scales explained much less of the variance; the best monthly model explained only 37.4% of the variance ($p=0.012$), while the best semi-monthly model explained 19.2% of the variance ($p=0.002$). The most likely explanation for this gradual increase is that as variability was reduced through data aggregation to broader time scales, the relationships between variables became stronger. As well, temporal autocorrelation decreased as time scales lengthened, solving another problem with the shorter time scale analyses. Thus, the best model was created at an annual scale. The next step after selecting the best model is to identify of possible mechanisms or pathways by which gray whale abundance is affected by the significant environmental variables.

Potential explanations of how the environmental variables relate to gray whale abundance

The results from the best multiple regression analysis showed that 89.6% of the variance in annual gray whale abundance was explained by two environmental variables; wind speed at La Perouse Bank and upwelling at 48ºN lagged two years. This indicates that there are biological pathways by which these two variables are affecting gray whale abundance on an annual scale. In very general terms, both variables are believed to affect gray whale abundance through affecting prey availability, both in an indirect manner. Upwelling brings cold, nutrient-rich deeper water to the surface, thus supplying nutrients for phytoplankton growth, which is then translated into zooplankton growth and as such to gray whale planktonic prey. Wind speed is assumed to affect several areas, including mixing of the euphotic layer, thus potentially reducing plankton productivity, and may have effects on the physical habitat of gray whale prey species

To further investigate the possible pathways by which the environmental variables affect gray whale abundance, it is important to review the biology of their prey. In the study area considered here, the main prey of foraging gray whales are mysids, small 'opossum shrimp'. Mysids are prey for higher trophic level predators (Mauchline 1980). Organisms which prey on mysids include rockfish [*Sebastes* spp.] (Turpen *et al.* 1994), flounder (Takahashi *et al.* 1999), perch [*Perca* spp.] (Granqvist & Mattila 2004), and sea birds (Cairns 1987). Mysids have also been identified as forage for the young of some species of fishes, particularly juvenile rockfish (Mauchline 1980, Singer 1985, Love *et al.* 1991), thus potentially playing an important role in rockfish recruitment in some areas. Due to their broad distribution and large number of species, mysids consume a wide variety of different organisms at different trophic levels, commonly including phytoplankton, zooplankton, and crustaceans (Tattersall 1951 cited in Stelle 2001, Mauchline 1980). Mysids may also consume organic debris, including kelp (Duggins *et al.* 1989), and even terragenous materials (Mauchline 1980), such as pollen (Bonsdorff & Bonsdorff 2005) when it accumulates in large quantities. In the northeastern Pacific, several studies have noted the use of kelp as food by mysids, indicating that this may be an important food source in this area (Schabes & Hamner 1992).

The life cycle of some mysids is poorly understood, although research has indicated that some mysid species have been observed to reproduce between 0.5 and 4 times per year (Mauchline 1980), thus indicating a wide variation in reproductive strategy (those with long generation times and those with short generation times). Stelle (2001) estimates that average time to maturity of gravid *H. sculpta* females is 73 to 81 days, having observed up to 4 generations per summer in her study area on the central coast of BC. Depending on the availability of food such as kelp during the summer, the production of mysids could be quite high and thus support gray whale feeding. The abundance of food should be directly or indirectly related to environmental conditions, providing an opportunity to try to link gray whale foraging with environmental variables through the food web.

Mysids are organisms that feed on many different items at a low trophic level (i.e. macroalgae, phytoplankton and perhaps zooplankton), which complicates the identification of mechanisms or pathways by which they are affected by environmental variables. One of the possible sources of food and shelter for mysids is kelp (Duggins *et al.* 1989, Schabes &

Hamner 1992), the production of which is influenced directly by environmental variables, such as nutrient availability (which could potentially be related to upwelling), sunlight quality and quantity, salinity, SST, wind and current speeds (Shields 1988, Carney 2003), and as such is expected to be affected by both variables in the best multiple model, wind speed at La Perouse and upwelling at 48°N lagged 2 years. Phytoplankton and zooplankton are also potential food sources for mysids (Mauchline 1980), and are expected to be affected by similar environmental variables. It is possible that mysids may feed on phytoplankton and small zooplankton in the water column, or on dead phytoplankton accumulating on the bottom as detritus. Overwintering mysids would likely need a food source, such as detritus perhaps from phytoplankton or kelp, to survive the winter. Two mysid species which occur off California, including one species also present off the central BC coast (Stelle 2001) were observed to consume the kelp blades directly and also the detritus of detached kelp (Schabes & Hamner 1992). Duggins *et al.* (1989) suggest that kelp detritus may play a role as a food source for mysids near islands dominated by kelp in the area of the Aleutian Islands. These three sources of food, phytoplankton, zooplankton and kelp, are all expected to be directly or indirectly affected by environmental variables.

Mysids are unlikely to be directly affected by wind speed due to their location at or near the bottom of the water column. However, kelp could be affected by wind speed, and it is possible that these effects would then be passed on to mysids residing on or near the kelp. If mysids were feeding on or living in kelp in a certain area and the kelp was removed or damaged by winds, the mysids would be expected to show a population decrease or lesser increase, given that they were using the kelp for forage and/or shelter. This is particularly possible since kelp in the study area has been observed to be perennial in some areas (Shields 1988), and as such would be affected by winter winds.

The dominant kelp in the study area, *Nereocystis luetkeana*, is attached to the substrate by a holdfast and stipe which is known to be susceptible to breakage when tidal forces exceed 0.1 ms^{-1} (Petrell *et al.* 1993), depending on the morphology and the size of the plants (Koehl 1986, Carrington 1990). If wind disturbances were to cause forces greater than 0.1 ms^{-1} to act on the kelp plants, then the kelp could be damaged or destroyed. Although *N. luetkeana* is believed to be very flexible and unusually extensible (Koehl & Wainwright 1977), the blades will not regrow once the upper stipe is destroyed or all the blades are

removed (Nicholson 1970), so even if storms damage the kelp without uprooting it, overall kelp production will still be decreased. It is also possible that windier/stormier conditions might affect kelp production through the movement of *N. luetkeana* sporophytes, which have been observed to migrate with currents, and are generally not well attached to the substrate in early months of the year (Maxell & Miller 1996). Since higher wind speeds are generally associated with larger waves, higher wind speeds could result in greater kelp detachment or removal of kelp sporophytes from suitable habitat thus reducing kelp production, while calmer conditions would increase kelp production. If kelp production is high in a particular year, it could provide a greater amount of forage and shelter for mysids, thus potentially increasing mysid production and thus foraging gray whale abundance, which would in turn relate well with the negative relationship between wind speed and gray whale abundance noted in the best annual model. Considering all the above information, I believe that this is a strongly possible potential pathway by which wind speed could affect gray whale abundance in the study area.

The relationship between kelp and mysids has been presented previously by other researchers. Turpen *et al.* (1994) hypothesize that sites that experience high levels of kelp removal during the winter would also experience decreases in *Holmesimysis costata* abundance, potentially due to a loss of sheltered habitat or a lost food source. Stelle (2001) notes that growth of mysids in two discrete bays in her study area was similar, but a third bay's mysids exhibited much slower growth. The third bay had much less kelp coverage than the other two bays, leading the author to postulate that primary productivity may have been lower in that area and that in years where there is less kelp due to storm disturbance, mysid growth may be slower. Further, kelp production has also been shown to be affected by broad temporal scale environmental events such as ENSO events (Edwards 2004, Edwards & Hernandez-Carmona 2005), indicating that its abundance is closely linked to environmental variables.

Two other possible trophic pathway to mysids, phytoplankton and zooplankton, would also be negatively affected by wind mixing. Phytoplankton production is expected to be affected by wind speed in a similar manner to kelp; that is that the relationships between wind speed and phytoplankton production is also expected to be negative, mainly due to a negative impact of wind mixing on the stability of the water column, reducing stratification

and mixing plankton, particularly phytoplankton, out of the euphotic zone where growth is faster due to higher temperatures and increased exposure to sunlight (Lalli & Parsons 1997). Increased phytoplankton abundance through stratification would provide a greater amount of prey for zooplankton (Lalli & Parsons 1997), in turn increasing their abundance. Mysids would benefit from the greater numbers of phytoplankton or zooplankton prey, and would thus be expected to increase their abundance as well. In this way, lower wind speeds may also be related to greater zooplankton and mysid abundance. Organic sediments may be resuspended in shallow coastal areas by both tidal action and wind mixing (Roman 1978, Grossart *et al.* 2004, West *et al.* 2005), making them available to organisms located low in the water column, such as hyperbenthic mysids. If mysids are overwintering for multiple years, then it is possible that bursts of phytoplankton production in particular years could be translated into greater production of mysids and thus greater gray whale abundance several years after. As the life span of the mysids in the study area is currently unknown, this idea remains speculative.

However, there are some limitations to this hypothesis. *N. luetkeana* is mainly an annual kelp, believed to be overwintering in most areas only in low numbers (Shaffer 2000, Chenelot *et al.* 2001), meaning that nutrients from the present year are would likely be most important to its growth and overall production. Through overwintering, it is possible that upwelling from the year before might play a role in terms of production of kelp that overwintered, but it is unlikely upwelling from two years prior could play a role in this specific hypothesis. As well, the decomposition time estimated for *N. luetkeana* ranges from 6 days for lamina to 14 days for stipes (Smith & Foreman 1984), making it impossible for decomposing kelp to have come from a previous year's production. However, kelp abundance dynamics and the effects of upwelling on kelp have not been investigated in the study area, and thus further investigation is necessary. As well, other locally present kelp species, such as Laminaria or Macrocystis, may be playing a role in the relationship, and their productions and life cycle may differ significantly from *Nereocystis*. It is also important to note that upwelling may be related to gray whale prey production in a way not immediately obvious. For this reason, this relationship would benefit from further research in the future.

An explanation for the importance of upwelling at 48ºN lagged 2 years is also not clear when the reproduction time of mysids is considered. Mysid reproduction is estimated to be at least 4 generations per summer for the geographically adjacent area of the central BC coast, and possibly more (Stelle 2001). Thus the time scale over which primary production (influencing kelp, phytoplankton and zooplankton supplies) would be likely to be important is more on the scale of weeks to months. It is interesting that no relationships between gray whale abundance and upwelling were noted at shorter time scales, as those scales are expected to have fit well with these aspects of the mysids' life histories. However, if mysids are overwintering, possibly over multiple years, then the lagged upwelling would be related to the amount of prey available to them, possibly in their early life stages, which could determine mysid abundance two years later, thus accounting for the two-year lag at a coarser temporal scale. Stelle (2001) does not discuss the abilities of mysids to overwinter, but it is a very strong possibility, given observations in other areas, such as those by Turpin *et al.* (1994), as well as given consideration of mysid life histories and generation times (Mauchline 1980). This may also be true if mysids are feeding on zooplankton; the amount of time needed for energy to pass to such higher trophic levels is estimated at several months (Denman *et al.* 1989), and thus the amount of time taken for the transfer of energy could potentially lengthen the time lags between changes in upwelling and when it is observed in changes to the abundance of gray whales.

It is important to note that the pathways of kelp or phytoplankton or zooplankton to mysids to whales may not be the only pathways by which gray whale abundance is affected by wind speed. A study on marine mammal abundance over the shelf and shelf break off California also found a strong negative relationship between marine mammal sightings and wind speed (Keiper *et al.* 2005). In that case, it is not likely that kelp played a significant role in passing environmental fluctuations to organisms observed far from shore and the habitats that macroalgae occupy, or it may simply be a coincidence that that study found the same result as this study in terms of wind speed (negative correlation, relatively strong relationship). In that study, it appears that the wind speed was related more to general ocean condition and structure (encompassing SST, wind speed, density, and thermocline depth), or upwelling events, which may be related to plankton production and thus prey availability for marine mammals (McGowan *et al.* 2003, Keiper *et al.* 2005).

In this study, tests of upwelling at other locations did not shed much more light on the role of upwelling in influencing gray whale abundance. Upwelling at 54ºN was highly predictive at the yearly scale; however, it was the current year that was significant, not at a lag of 2 years as other upwelling variables (45ºN and 48ºN) were. How upwelling measured more than 6º north of the study area could be spatially related to local gray whale abundance is unknown, and there is the possibility that the results for these distant upwelling variables are erroneous. However, the fact that upwelling at 45ºN is also significant at a lag of 2 years at 48ºN indicates that the results are probably not erroneous; rather, they are inexplicable given our current knowledge of this particular food web and interactions within it. Unidentified "black box" processes operating between the gray whale abundance and the environmental variables could be responsible for the lack of understanding of the role of upwelling at 48ºN lagged 2 years or of upwelling measurements from different areas.

…and why some were not significant

Interestingly, many variables were not significant at any temporal scale. This indicates that such variables are either significant at another temporal scale, that there are no linear relationships between these variables and the gray whales, or they simply are not related to gray whale abundance. Examples of such variables include salinity at Amphitrite and upwelling at 51ºN.

It is completely possible that salinity is not a strong control on local plankton production, as salinity mainly affects the sinking rates of phytoplankton, influencing the density of seawater and affecting the ability of phytoplankton to stay in the euphotic layer, thus increasing their exposure to sunlight and increasing overall phytoplankton production. Salinity is not expected to vary a great amount at Amphitrite, but at Nootka it might vary due to due to runoff and river discharge; this is perhaps why salinity at Nootka was significant in the single regressions at a monthly scale; however, the amount of variance explained was low (10.0%).

Upwelling at 51ºN may not be related to whale abundance due to the distance from the study area of the measurements (~ 3º north of the study area). However, this is not necessarily the best explanation, as upwelling further north at 54ºN was highly explanatory (R^2=0.633, p=0.018) at a yearly scale. Thus, the only conclusion that can be made is that the

upwelling at the area near 51ºN is unrelated to gray whale abundance in the study area at the scales examined in this study.

It is surprising that sunlight was not a more influential variable in the regression analyses which were run for this study. The productivity of zooplankton, and through this gray whale abundance, was expected to be linked to sunlight at some scale, most likely the monthly or annual scale, due to the role of sunlight in the growth of organisms at the base of the food chain, particularly phytoplankton and kelp. It was thus expected that sunlight would have an effect on gray whale abundance, particularly over finer temporal scales which may be important during zooplankton growth to maturity. There are several possible explanations as to why the results indicated no relationship. First, other factors, such as wind speed, may be stronger influences on the abundance of prey, making the effect of sunlight rather insignificant in comparison. Second, it is also possible that zooplankton, such as mysids, are not feeding directly on phytoplankton or kelp to a great extent, and thus that pathway is less significant than anticipated. Third, it is possible that none of the temporal scales examined here are the one at which sunlight is affecting phytoplankton and macroalgae. Fourth, unidentified black box processes may be operating between sunlight and the zooplankton prey of gray whales, making the pathway not as straightforward as it might theoretically seem. These types of 'black box' scenarios, where connections between variables are expected but do not materialise, require further exploration. Identification of such 'black box' processes will move science closer to a precise understanding of the pathways between trophic levels and food web dynamics in general.

Why didn't the regression equation create better predictions on shorter time scales?

Short time scales have been expected to be important in terms of the life histories of gray whale prey, such as mysids, so why didn't variables perform better at shorter time scales? There are several reasons why the regression equation failed to adequately describe shorter-time scale relationships between gray whale abundance and environmental predictor variables.

First, the amount of variability in the data at shorter time scales may have made it impossible identify a relationship with this analysis, or a relationship simply may not be present in data with such high variability. When the data were aggregated over a longer time

scale, variability was averaged out, likely resulting in a better fit of the regression line to the data. This can be observed through the amount of variance explained by the multivariate models increasing at each time scale from 19.2% at the semi-monthly scale to 37.4% at the monthly scale to 89.6% at the yearly scale.

Second, unidentified black box processes may be acting between the environmental variables and the gray whale abundance. This means that the influences of environmental variables on processes, such as phytoplankton or zooplankton growth, may be affected by other unidentified variables which were not examined in this study.

Third, completely different variables which were not used in this analysis may be acting on the abundance of whales at shorter time scales. This study included some basic environmental variables assumed to be influential in a very nearshore environment, but future studies are certainly warranted to investigate other independent variables.

Fourth, the time scales examined may not have been those at which relationships occur. Other time scales which have the potential to be important but which were not examined include multi-annual or seasonal time scales. The seasonal time scale was not examined here due to the potential ambiguity of separating the year into seasons; however, several organisations of data by season with different numbers of seasons might prove to be of interest.

Fifth, time lags between the environmental variables and gray whale abundance may not have been static over the length of this study, especially since Stelle (2001) observed that juvenile mysids were released at different times in different years (one to two weeks difference). This would result in a type of match-mismatch situation where in some years the time period used for the analysis would be appropriate to encompass the event in question, while in other years the event would take longer or occur at a different time. This would result in a mismatch and thus no relationship between the independent and dependent variables in those years, while strong relationships would be present in other ‘match’ years, creating a relationship which does not hold up in all years. This could explain why shorter time scale data was less well related to gray whale abundance. This does not mean that time lags do not play an important role; rather, it indicates that they may be of variable length.

Time lags

Time lags were expected to be an important part of the gray whale-environmental variable relationship, but little evidence of their presence was observed in the results of the single regressions on the shorter time scale data, particularly the weekly data. The shorter time scale data were where the greatest role of time lags was expected, particularly considering the approximate time to maturity of some species of mysids is of 73-81 days (Stelle 2001).

Time scale	Variable	Lag in days	R^2	p
Semi-month	Wind speed La Perouse Bank – lagged 3 periods	42	0.104	0.009
Month	Wind speed La Perouse Bank – lagged 2 months	60-62	0.141	0.024
Month	Sunlight Tofino – lagged 12 months	365	0.104	0.055
Year	Upwelling 48°N – lagged 2 years	730	0.457	0.066
Year	Upwelling 45°N – lagged 2 years	730	0.552	0.035

Table 10. Explanatory variables exhibiting time lags in single regressions. Time scales at which the analyses were conducted are listed in the Time scale column; independent variables are listed in the 'Variables' column; the length of the lag revealed by the analyses is listed in the Lag in days column; the R^2 column represents the R^2 value of the regression and the 'p' column lists the significance of each regression.

The annual scale data showed that 45.7% of the variance was explained by upwelling at 48ºN lagged 2 years. This is the greatest amount of variance explained by a lagged variable, other than upwelling at 45ºN ($R^2 = 0.552$, $p = 0.035$), which was not included in the original analysis; all other lagged variables at other time scales explained 10-14% of the variance. Thus, other than at a yearly scale, lagged variables did not add much explanatory power to the regression equation. The length of lag at the yearly scale may be related to the overwintering of gray whale prey such as mysids, if they do overwinter for two winters, then this would make biological sense. The main issue is that there is information lacking in terms of the current knowledge on mysid life histories, for example, where it is known that four generations are being produced in a single summer by one species (Stelle 2001), but little or no information is available on the organism's life span. In this case, it could be expected that upwelling at shorter time scales when mysid growth was occurring would also be important; however, this did not fall out in the analysis. Thus, it is not always

straightforward to disentangle the relationships between variables, particularly when they are separated by several trophic levels in the food web.

In some cases, time lags were not observed in association with variables which were expected to exhibit them. Time lags of SST were expected but not observed other than a very weak relationship between gray whale abundance and SST at Nootka lagged 12 months ($R^2 = 0.079$, $p = 0.097$). The expectation was that a SST-whale abundance time lag would have been obvious at a monthly temporal scale within the first 3 months due to the effects of SST on seasonal events, for example, the spring phytoplankton bloom. Higher SSTs earlier in the spring were expected to increase the phytoplankton production (and thus zooplankton production, and thus gray whale prey) later the same summer, and thus a lag of several months would be apparent. It may be that the spring bloom is not an important event in terms of prey abundance for gray whale prey, or that a black box process occurs between phytoplankton and zooplankton; this could even be a time lag incorporating time for small zooplankton to assimilate phytoplankton. The identification of time lags in the trial-and-error manner used here can only allow the conclusion that time lags were not observed at the temporal scales tested. Other untested temporal scales cannot be commented on and remain open to speculation, and thus although they were not observed here, they may still exist.

Overall, time lags are known to be important in marine systems (Duarte 1990), and their presence is demonstrated in this study at several time scales, although the importance of lagged variables as predictors was not as great as expected, particularly in terms of SST, and at short time scales. However, it is also possible that time lags were not identified due to variable length lags at different times of year. Thus, it is possible to conclude that time lags are present in this system, but conclusive evidence regarding their length is not identified here, other than at a yearly scale.

Scale and scale-coupling

The study of scale and the coupling of data recorded at different spatial scales has been recognised as one of the great necessities of any ecological study and is considered to be an area of scientific inquiry needing attention (Powell 1989, Steele 1989). Through relating oceanographic data collected at broad spatial scales to gray whale abundance data collected at a fine spatial scale, the concept of scale coupling is tested. Scale coupling is

expected to be present to some extent through the food web, since environmental variables are expected to exert substantial influence over production at lower trophic levels (Powell 1989); in this case gray whales' zooplankton prey and their prey. Only very spatially broad environmental variables were tested here, which may or may not represent oceanographic or environmental influences on the base of the food web over the fine scale of the gray whale abundance data. This was the drawback of not having independent and dependent data availability at multiple scales, which meant that data at two different scales was used for each regression, i.e. broad scale independent data, fine scale dependent data. It is considered desirable to have data at as many scales as possible to test for relationships (Steele 1989), but in this case, these were the only data available.

A main question of this study is: how related are broad scale oceanographic variables to top-predator abundance over a fine spatial scale area? These data only show strong effects of scale coupling at one temporal scale, the annual scale. The strong explanatory relationship at an annual scale between the environmental variables and gray whale abundance indicates that scale coupling occurs at this coarse temporal scale. In terms of shorter time periods, the dependent (gray whale abundance) data at a fine spatial scale do not relate well to the independent data (environmental variables) at broader spatial scales, perhaps due to the greater variability present in data aggregated over shorter time periods. It is also important to note that the time scales at which these data are aggregated may not be those at which broad scale oceanography is strongly related to gray whale abundance.

As it appears that scale-coupling is possible, and occurs in the data analysed here, the main question remaining is: how does scale coupling work to couple environmental variables and gray whale abundance? There is no true and hard pathway identified in this study by which environmental variables affect gray whale abundance, but the potential links between the two, such as phytoplankton, zooplankton and kelp, are discussed above. However, there are some other possible explanations for the scale coupling. In some cases, physical (environmental variables) and biological (gray whale abundance) scale coupling, such as that studied here, is the result of interactions of biological oceanography with topography. Canyons may provide a topographic disturbance in the water column, which in turn may affect phytoplankton production in the local area, providing a link between broad scale oceanography and fine scale topography which is manifested in plankton production (Ryan *et*

al. 2005). Topography was not a variable studied in this research, primarily since gray whales are more associated with shallow depth contours rather than unusual topography affecting primary productivity. Physical-biological scale coupling may also be related to broad-scale oceanographic events, such as ENSO events. Chavez *et al.* (1998) report on coupling between oceanographic variables and phytoplankton production in relation to ENSO events, showing that primary production in some areas is reduced by as much as 50% during certain phases of the ENSO. Thus, broad scale environmental events have effects on local primary production, which should then be translated into changes in prey abundance at finer spatial scales, such as the one examined here, for higher trophic level predators such as marine mammals. This study did not specifically investigate the effects of ENSO events on gray whale abundance, but a review of gray whale abundance in 1997/98 when a strong El Niño occurred shows that gray whale abundance was high in 1998. Therefore, there may have been an effect on the production of gray whale prey through increased phytoplankton or kelp production which resulted in a greater abundance of zooplankton and thus of gray whales. However, this is purely speculation, as there are no data available for primary production and zooplankton abundance in the study area during that period.

Other studies have attempted to identify the spatial scales at which marine mammal abundance is related to environmental or prey variables. However, these studies have generally focussed on wide-ranging marine mammals over broad spatial scales, such as elephant seals and sperm whales (Jaquet & Whitehead 1996, Bradshaw *et al.* 2002), and thus the results generally show that these organisms are best studied at broader spatial scales as would be expected. For gray whales, which have been observed to be both coastal and fine-scale foragers (see for example Murison *et al.* 1984, Dunham & Duffus 2001), the best scale at which their abundance should be studied in relation to foraging is not clear. This study attempts to link broad spatial scale predictive data to fine scale response data and thus doing so, tests whether or not the spatial scales are useful in terms of explaining gray whale abundance. At a fine spatial scale, such as the one used in this study, gray whales enter and exit the study area fairly often over short time scales. As such, it is important to note that gray whales may travel what seem to humans to be large distances over broad spatial scales, when in fact they may be small distances for a whale that migrates several thousand kilometres annually. Thus, although gray whale foraging is generally studied over fine scale

areas, it is relatively easy for gray whales to move to another nearby foraging area which may exhibit greater prey abundance. Thus, it is possible that the use of abundance data collected at a broader spatial scale, such as the west coast of Vancouver Island, would yield different results in terms of relationships between environmental variables and gray whale abundance.

Relatedness of gray whale foraging by time period

The results of the single regressions indicate that the number of gray whales in preceding periods is strongly related to the current period at several different time scales. The strength of the relationship was dependent on time scale, with the strongest relationships being at the shortest time scales, and the weakest relationships being at longer time scales. The strongest relationship was at the weekly scale, where the previous week's whales per survey (whales per survey lagged 1 week) explained 63% of the variance ($p=0.000$). At the semi-monthly and monthly scales, the previous period's whales per survey explained 51.2% of the variance ($p=0.000$), and 10.5% of the variance ($p=0.055$) respectively. At a yearly scale, the previous year's whales per survey only explained 1.4% of the variance and was not significant ($p=0.800$).

These results point to the abundance of whales in the study area being a seasonal phenomenon rather than a weekly, semi-monthly or monthly phenomenon due to the positive correlation between gray whale abundance and previous gray whale abundance. As well, the lack of relationship between and explanatory power of the previous year's whales per survey on the current year's whales per survey indicates that the number of whales present in one year is little influenced by or related to the number of whales the year prior, indicating that other factors, such as "bottom-up" environmental variables, are more influential on gray whale abundance than "top-down" predation pressures. These results are not what was expected, which was to see top-down pressures playing a role on an annual or monthly scale as gray whales fed upon zooplankton "stocks" and (theoretically) depleted them These results indicate that gray whale prey abundance is not severely affected by the amount of gray whale foraging between time scales of any length. Although mysid populations may be depleted in terms of not being an energetically viable prey source for gray whales, it seems that gray whales are not depleting the local population to a point where it cannot recover,

which has been suggested for other prey species, such as amphipods, within the study area and in other foraging areas (Highsmith & Coyle 1992, Dunham & Duffus 2001). Thus, these results indicate that gray whale abundance is a monthly or seasonal phenomenon, rather than being strongly directed by previous gray whale foraging.

Variables not included in these analyses

The poor results of the regressions over shorter time scales may also be due to the omission of important predictor variables from the analysis, as other variables might have explained a large amount of the variance that is currently unaccounted for in the models presented here. However, due consideration has been given to food web dynamics, and theoretically important environmental forcing factors were included in this analysis. Other variables related more closely to climate may explain other parts of the variance, for example the amount of local rainfall, or the Pacific Decadal Oscillation (PDO). Other studies have shown correlations between time series of upper-trophic level predators and the PDO, but such examples are generally characterised by longer time series of data than the gray whale data used here; see for example (Clark & Hare 2002), who used a time series of ~80 years. Thus, the gray whale data series used here is too short to allow the use of a decadal measure such as the PDO, it could be misleading to use such an index in a regression where the time period is very short (i.e. month, semi-month, week), or even with the yearly data since this series is shorter than a decade, the temporal measurement inherent in the PDO.

Assessing the amount of nutrients available to the very nearshore waters and nutrient concentrations at the fine scales studied in this research is also important. One way to measure nutrient supply in the coastal environment, other than by upwelling, is to measure rainfall. The amount of rainfall is related to the amount of runoff; runoff carries nutrients from land into the ocean, and is thus a potential measure of nutrient supply to coastal oceans. Another way to measure nutrient supply would be to assess the amount of nutrients available through examining the streams themselves. Research in the study area on this topic has already been completed; the results indicated that while streams have the ability to act as conduits for nutrients from watersheds to stream mouths, much of the nutrient load is recycled prior to reaching the stream mouth, and thus runoff does not always contain a large amount of nutrients (Karagatzides 2006). However, it would still be informative to have

measures of nutrient concentration in runoff to use as a predictor of gray whale abundance, if simply to be able to exclude nutrients sourced from runoff as not being an important predictor of gray whale abundance in this area.

Another parameter which would have been of interest to this study is primary productivity. Other researchers have noted correlations between primary productivity measurements and marine birds and mammals (Benson *et al.* 2002, Littaye *et al.* 2004, Yen *et al.* 2005). Numeric measures of broad scale primary productivity, such as chlorophyll A or nitrate concentration, were unavailable. Remotely sensed data offer an option to assess broad spatial scale primary productivity through chlorophyll A concentration recorded by sensors such as SeaWiFS. SeaWiFS scenes covering southern coastal BC are available over the internet through Fisheries and Oceans Canada, but upon close inspection, the coverage was observed to be of poor temporal resolution over some periods, and thus the use of SeaWiFS scenes over short time scales was not always possible. Also, cloud often covers the study area, particularly in early spring and late summer, and this reduced the number of potential scenes to an even greater extent. It is possible that, if a system of rating or categorizing the scenes in terms of chlorophyll A concentration were devised, a categorical variable could be created to measure primary productivity, although it would be subject to the restrictions on data availability discussed above.

Thus, there are several additional variables which would have been complementary to this analysis and may be of further interest in the future. However, statistically, the present equation adequately describes the relationship between environmental variables for the present research.

Predicting future gray whale abundance

By using the regression model created here, it is possible to test the results of the regression in terms of creating a model capable of describing gray whale abundance in future years with some accuracy. Although it is exciting to have a potential predictive model for gray whale abundance, it is also important to treat the results of modelling exercises with caution, as even detailed models may fail to adequately represent the variability inherent in marine systems, especially at fine spatial scales (Helbig & Pepin 2002), such as this one. Also, it must be taken into consideration that although 89% of the variance was explained by

the annual multiple model, 11% of the variation must be explained by other variables and as such, any projections for future whale abundance may not be perfectly accurate; this could only be achieved if the regression equation explained 100% of the variance. As well, relationships between time series of environmental variables and organisms often turn out to be ephemeral (DeYoung *et al.* 2004b), and thus even the strong explanatory results and highly predictive multiple regression models obtained from the annual multiple regression should be treated with caution in terms of their application to future gray whale abundance.

It is also important to note that although the equation created here can explain the variance in abundance of gray whales with relatively good accuracy, the equation is not truly predictive since it requires the input of yearly average values of environmental variables including months after gray whales have left the study area. Thus, estimates of future yearly values for the independent variables have to be used in any attempt to predict gray whale abundance with the regression model created here. This is less simple and straightforward than if variables were organised by month, i.e. January SST, February SST, etc., where data recorded early in the year could be used to predict summer gray whale abundance. Investigations into aggregating the data in the opposite manner, by year, season and month by year – i.e. January SST, February SST, etc. – were conducted, but scatterplots and Pearson's correlation tests showed no significant relationships between gray whale abundance and environmental variables. Thus, this study is more useful to identify which environmental variables are related to gray whale abundance than to create a predictive model.

Conclusions

Model fit and characteristics

Overall, the fit of the best regression model can be described as very good; explaining 89.6% of the variance in gray whale abundance. The main caveat to the high explanatory power of the yearly model is that the process by which the environmental variables are affecting gray whale abundance is not well understood, and that the number of observations regressed is low. Shorter analyses offered less explanation of the variance, with no models explaining more than 40% of the variance. Shorter temporal scale multiple models, such as those created at the semi-monthly scale were also characterised by greater levels of temporal autocorrelation, which contradicts one of the main assumptions of regression analysis.

Overall conclusions

The main conclusions of this research are as follows. First, the variables representing wind speed at La Perouse Bank and upwelling at 48ºN lagged 2 years measured at an annual scale explain the most variance in gray whale abundance of all combinations of independent variables at all time scales tested. The effects of variable wind speed on gray whales are expected to be felt through the food web mainly via alterations to phytoplankton, zooplankton and kelp production, as gray whale prey are hypothesised to be reliant on these sources for food and shelter in the study area. The mechanism by which upwelling at 48ºN lagged 2 years affects gray whale abundance unclear, although it is possible that gray whale prey such as mysids are overwintering several years and this is the reason behind the relationship.

Second, scale coupling was observed in these analyses, but only at the temporally coarse annual scale. Strong scale coupling at much shorter time scales was expected, mainly due to the production of multiple generations of mysid species in one summer noted by Stelle (2001). For this reason, it was expected that weekly, semi-monthly and monthly analyses would reveal strong relationships and thus strong scale coupling with environmental variables, but they did not. It is possible that scale coupling simply does not work well on fine temporal scales for these data, and that the use of finer scale oceanography in relation to fine scale gray whale abundance might offer more explanatory power, or that mysids live

longer than expected and thus coarser temporal scale data applies more adequately to their life history.

Third, identifying time lags through testing data at multiple temporal scales and multiple lags with regression analysis was tested here and met with some success. At all time scales, lagged variables explained some of the variance, but the only large amount of variance explained was by upwelling at 48ºN lagged 2 years at the annual scale. It appears that time lags play a role in the structure of the food web and are likely a common characteristic of interactions between the trophic levels discussed here, but the probability of identifying all time lags in the manner employed here is unlikely, and as such there are probably more time lags involved in the food web which were not noted here.

Fourth, there was little observed effect of top-down pressures on gray whale abundance from previous gray whale foraging, due to positive correlations between gray whale abundance over time periods indicating a monthly or seasonal effect rather than a negative correlation between time periods, which would have indicated top-down pressures. Although these results could lead to the conclusion that gray whale foraging in the study area does not reduce the amount of prey to such an extent that it negatively affects future gray whale foraging, observations in the field show that this is in fact the case. With the data at the scales investigated here, no effects are shown, so these effects must occur at different time scales than those investigated here, perhaps at a bi-yearly time scale or a seasonal time scale.

Fifth, similarities to other marine mammal studies are present. Gray whale abundance is highly variable in time and space, as has been noted for fin, sperm and blue whales (Jaquet & Whitehead 1996, Littaye *et al.* 2004, Croll *et al.* 2005), and as in those cases is related to environmental variables which are expected to act as forcing factors. The current analyses also revealed a similar relationship to that noted by Keiper *et al.* (2005) between wind speed and marine mammal abundance. Wind speed was one of two highly predictive variables used in this study's best multiple regression model. However, it is unlikely that the environmental mechanism behind the similar results is the same for these two studies.

Sixth, both levels of the food web under consideration are thought to be prey switchers (gray whales and gray whale prey), following the ephemerality of relationships

noted by deYoung *et al.* (2004a). This makes it difficult to construct a model which accurately describes interactions between environmental variables and gray whale abundance. As well, pathways between environmental variables and gray whales will vary depending on prey choice at each level of the food web, and therefore will likely also vary with prey availability. The results of this study should not be taken as the only possible manner by which gray whale abundance is affected by environmental variables.

Recommendations for future research

There are several recommendations for further research which arose out of this project. They are not concentrated in one part of the research, but rather are drawn from diverse sections and objectives of this study.

First and foremost is the search for other variables which may add to the multivariate regression models at all time scales, particularly at the shorter time scales. Knowledge of primary production would add to our understanding of the effects of environmental variables on phytoplankton and kelp production, and thus on zooplankton production. The inclusion of such information will give a broader understanding of which variables are strongly related, and particularly those which are not related, to help narrow the focus to the few important variables that are driving these food web interactions, leading to better modelling results.

Further information on nutrient supply to these very nearshore waters is also an area which could benefit from further scientific examination. The effects of nutrient supply from all land sources in the study area have not been quantified, and the effects of events such as runoff and peak discharge on local oceanography and thus on local prey populations should be examined. Knowing the dispersal of nutrients supplied to the nearshore waters through runoff would also help to understand fine spatial scale variations in prey (Cowles *et al.* 1998). These topics tie in with the need for more research on upwelling over shorter temporal and much finer spatial scales. An overall picture of nutrient supply from all sources and dispersal within the study area would promote a greater understanding of fine spatial scale nutrient dynamics within and between years.

Also of research interest is the resolution of the pathways, or black boxes, by which gray whale prey abundance is affected by the environmental variables studied here. Although possible explanations of the pathways by which prey might be affected by these

variables have been offered here, the topic is still open to further speculation or confirmation through other research. These black box processes are one of the most important facets of this research, and thus should drive future research in relating marine mammal abundance to environmental, oceanographic or even atmospheric variables.

The issues of temporal scale and time lags also demand more attention. A time scale which was not examined here but may be of interest is the seasonal time scale, where the data would be aggregated into several distinct seasons per year. A seasonal analysis might more accurately capture the effects of variables that did not fall out well in this analysis, including sunlight, and it might also provide the opportunity to identify additional time lags. Cross-correlation analysis may hold some potential for identifying other time lags, as may time series analysis, which also allows for the identification of time lags whose length varies year to year. The current analyses cannot identify such time lags in the data. An accurate knowledge of time lags is integral to our understanding of how food webs work and the roles of each component of the food web. Further research will also clarify the role of variable length time lags, in terms of identifying when predator and prey are well or poorly matched in terms of production, resulting in a better understanding of the highly variable or patchy overall abundance of organisms observed at higher trophic levels. Through this knowledge, we will gain a better understanding of how food webs function, which will encourage further identification and incorporation of the black box processes into our current knowledge.

Mysids in general could also benefit from further intense research. That these organisms occupy such a vital space in the food web, and are expected to prey on and be predated on by many organisms (Mauchline 1980), is reason enough for further in depth studies of mysid-centric topics. The fact that the prey and predators of most mysid species are only generally or randomly known is another strong reason to warrant further study. Mysid life histories are also poorly understood; Mauchline (1980) provided the most recent English-language review, although a more recent Japanese review exists (Takahashi 2004); thus a more up-to-date English review is necessary, particularly for such a varied group of organisms. Further habitat studies on the species in the study area could also provide important information on other unexplored areas such as the role of kelp, as to whether it is most important as a shelter or food resource.

The final area where future study is important is to repeat a similar modelling study in other tertiary foraging areas used by gray whales. Further investigation of how gray whale abundance is determined in other areas and at other times, possibly with different prey, will further our understanding of the interactions between environmental forcing variables and gray whale abundance over broader scales. Different processes or pathways probably link environmental variables and gray whales in different areas, particularly due to the foraging plasticity of both gray whales and their primary prey in tertiary foraging areas, the mysids. Further research similar to this study will enable the documentation of the food web dynamics in other areas, allowing for comparisons with the present study.

Literature Cited

Anderson, P.J., J.E. Blackburn, and B.A. Johnson. 1997. Declines of forage species in the Gulf of Alaska, 1972-1995, as an indicator of regime shift. *In* Forage Fishes in Marine Ecosystems; Int. Symp. on the Role of Forage Fishes in Marine Ecosystems, Anchorage, Alaska (USA), 13-16 Nov 1996. *Edited by* American Fisheries Society, Fairbanks, Alaska. pp. 531-543.

Anderson, P.J. 2000. Pandalid shrimp as indicators of marine ecological regime shift. *Journal of Shellfish Research,* **19**(1): 549.

Andrade, H.A. & C.A.E. Garcia. 1999. Skipjack tuna fishery in relation to sea surface temperature off the southern Brazilian coast. *Fisheries Oceanography,* **8**(4): 245-254.

Bailey, K.M. 2000. Shifting control of recruitment of walleye pollock *Theragra chalcogramma* after a major climatic and ecosystem change. *Marine Ecology Progress Series,* **198**: 215-224.

Bence, J.R. 1995. Analysis of short time series - correcting for autocorrelation. *Ecology,* **76**(2): 628-639.

Benson, A.J. & A.W. Trites. 2002. Ecological effects of regime shifts in the Bering Sea and eastern North Pacific Ocean. *Fish and Fisheries,* **3**(2): 95-113.

Benson, S.R., D.A. Croll, B.B. Marinovic, F.P. Chavez, & J.T. Harvey. 2002. Changes in the cetacean assemblage of a coastal upwelling ecosystem during El Nino 1997-98 and La Nina 1999. *Progress in Oceanography,* **54**(1-4): 279-291.

Bienfang, P.K. & J.P. Szyper. 1982. Effects of temperature and salinity on sinking rates of the centric diatom *Ditylum brightwelli*. *Biological Oceanography,* **1**(3): 211-223.

Bleiker, W. & F. Schanz. 1997. Light climate as the key factor controlling the spring dynamics of phytoplankton in Lake Zurich. *Aquatic Sciences,* **59**(2): 135-157.

Bonsdorff, E. & B. Bonsdorff. 2005. Mass-occurrence of pollen-feeding mysid shrimp *Neomysis integer* (Leach, 1814), Crustacea: Mysidacea. *Memoranda Societatis Pro Fauna Et Flora Fennica,* **81**(1): 41-43.

Bradshaw, C.J.A., M.A. Hindell, K.J. Michael, & M.D. Sumner. 2002. The optimal spatial scale for the analysis of elephant seal foraging as determined by geo-location in relation to sea surface temperatures. *ICES Journal of Marine Science,* **59**(4): 770-781.

Cairns, D.K. 1987. Diet and foraging ecology of black guillemots in northeastern Hudson Bay. *Canadian Journal of Zoology,* **65**(5): 1257-1263.

Calambokidis, J., J.D. Darling, V. Deecke, P. Gearin, M. Gosho, W. Megill, C.M. Tombach, D. Goley, C. Toropova, & B. Gisborne. 2002. Abundance, range and movements of a feeding aggregation of gray whales (*Eschrichtius robustus*) from California to southeastern Alaska in 1998. *Journal of Cetacean Research and Management,* **4**(3): 267-276.

Carney, L.T. 2003. Restoration techniques for *Nereocystis luetkeana* (Mertens) Postels Et Ruprecht (Bull Kelp). *Journal of Phycology,* **39**(S1): 7.

Carrington, E. 1990. Drag and dislodgment of an intertidal macroalga: Consequences of morphological variation in *Mastocarpus papillatus* Kuetzing. *Journal of Experimental Marine Biology and Ecology,* **139**(3): 185-200.

Chenelot, H., J. Matweyou, & B. Konar. 2001. Investigation of the overwintering of the annual macroalga *Nereocystis luetkeana* in Kachemak Bay, Alaska. University of Alaska Sea Grant: P.O. Box 755040 205 O'Neill Bldg. Fairbanks AK 99775-5040 USA, [URL:http://www.uaf.edu/seagrant/]. pp.19-24.

Clark, W.G. & S.R. Hare. 2002. Effects of climate and stock size on the productivity of Pacific halibut. American Fisheries Society: 5410 Grosvenor Ln. Ste. 110 Bethesda MD 20814-2199 USA, [URL:http://afs.allenpress.com].

Clutter, R.I. 1969. The microdistribution and social behaviour of some pelagic mysid shrimps. *Journal of Experimental Marine Biology and Ecology,* **3**: 125-155.

Cowles, T.J., R.A. Desiderio, & M.-. Carr. 1998. Small-scale planktonic structure: persistence and trophic consequences. *Oceanography,* **11**(1): 4-9.

Croll, D.A., B. Marinovic, S. Benson, F.P. Chavez, N. Black, R. Ternullo, & B.R. Tershy. 2005. From wind to whales: trophic links in a coastal upwelling system. *Marine Ecology Progress Series,* **289**: 117-130.

Croll, D.A., B.R. Tershy, R.P. Hewitt, D.A. Demer, P.C. Fiedler, S.E. Smith, W. Armstrong, J.M. Popp, T. Kiekhefer, V.R. Lopez, J. Urban, & D. Gendron. 1998. An integrated approach to the foraging ecology of marine birds and mammals. *Deep-Sea Research Part II -Topical Studies in Oceanography,* **45**(7): 1353-1371.

Curtis, K.A. 2004. Fine scale spatial pattern of Pacific sardine (*Sardinops sagax*) and northern anchovy (*Engraulis mordax*) eggs. *Fisheries Oceanography,* **13**(4): 239-254.

Denman, K.L., H.J. Freeland, & D.L. Mackas. 1989. Comparisons of time scales for biomass transfer up the marine food web and coastal transport processes. *In,* Effects of Ocean Variability on Recruitment and an Evaluation of Parameters Used in Stock Assessment. *Edited by* R.J. Beamish and G.A. McFarlane. *Can. Spec. Publ. Fish. & Aquat. Sci.* **108**.

DeYoung, B., R. Harris, J. Alheit, G. Beaugrand, N. Mantua, & L. Shannon. 2004a. Detecting regime shifts in the ocean: data considerations. *Progress in Oceanography,* **60**(2-4): 143-164.

DeYoung, B., M. Heath, F. Werner, F. Chai, B. Megrey, & P. Monfray. 2004b. Challenges of modeling ocean basin ecosystems. *Science,* **304**(5676): 1463-1466.

Draper, N.R. & H. Smith. 1998. Applied regression analysis, 3rd ed. Wiley Interscience: New York, USA. 736 p.

Duarte, C.M. 1990. Time lags in algal growth: generality, causes and consequences. *Journal of Plankton Research,* **12**(4): 873-883.

Duffus, D.A. 1996. The recreational use of gray whales in southern Clayoquot Sound, Canada. *Applied Geography,* **16**(3): 179-190.

Duggins, D.O., C.A. Simenstad, & J.A. Estes. 1989. Magnification of secondary production by kelp detritus in coastal marine ecosystems. *Science,* **245**(4914): 170-173.

Dunham, J.S. & D.A. Duffus. 2002. Diet of gray whales (*Eschrichtius robustus*) in Clayoquot Sound, British Columbia, Canada. *Marine Mammal Science,* **18**(2): 419-437.

Dunham, J.S. & D.A. Duffus. 2001. Foraging patterns of gray whales in central Clayoquot Sound, British Columbia, Canada. *Marine Ecology Progress Series,* **223**: 299-310.

Edwards, M.S. 2004. Estimating scale-dependency in disturbance impacts: El Niños and giant kelp forests in the northeast Pacific. *Oecologia,* **138**(3): 436-447.

Edwards, M.S. & G. Hernandez-Carmona. 2005. Delayed recovery of giant kelp near its southern range limit in the North Pacific following El Nino. *Marine Biology,* **147**(1): 273-279.

Gallego, A., M.R. Heath, E. McKenzie, & L.H. Cargill. 1996. Environmentally induced short-term variability in the growth rates of larval herring. *Marine Ecology Progress Series,* **137**(1-3): 11-23.

Granqvist, M. & J. Mattila. 2004. The effects of turbidity and light intensity on the consumption of mysids by juvenile perch (*Perca fluviatilis* L.). *Hydrobiologia,* **514**(1-3): 93-101.

Greene, C.H. & A.J. Pershing. 2000. The response of *Calanus finmarchicus* populations to climate variability in the Northwest Atlantic: basin-scale forcing associated with the North Atlantic Oscillation. *ICES Journal of Marine Science,* **57**(6): 1536-1544.

Grossart, H., T. Brinkhoff, T. Martens, C. Duerselen, G. Liebezeit, & M. Simon. 2004. Tidal dynamics of dissolved and particulate matter and bacteria in a tidal flat ecosystem in spring and fall. *Limnology and Oceanography,* **49**(6): 2212-2222.

Hair, J.F.J., R.E. Anderson, R.L. Tatham, & W.C. Black. 1998. Multivariate data analysis, 5th edition. Prentice Hall: Upper Saddle River, NJ, USA. 730 p.

Hare, S.R. & N.J. Mantua. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Progress in Oceanography,* **47**(2-4): 103-145.

Helbig, J.A. & P. Pepin. 2002. The effects of short space and time scale current variability on the predictability of passive ichthyoplankton distributions: an analysis based on HF radar observations. *Fisheries Oceanography,* **11**(3): 175-188.

Highsmith, R.C. & K.O. Coyle. 1992. Productivity of Arctic amphipods relative to gray whale energy requirements. *Marine Ecology Progress Series,* **83**(2-3): 141-150.

Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs,* **54**(2): 187-211.

Hyrenbach, K.D. & R.R. Veit. 2003. Ocean warming and seabird communities of the southern California Current System (1987-98): response at multiple temporal scales. *Deep-Sea Research Part II - Topical Studies in Oceanography,* **50**(14-16): 2537-2565.

Ishizaka, J., M. Takahashi, & S. Ichimura. 1983. Evaluation of coastal upwelling effects on phytoplankton growth by simulated culture experiments. *Marine Biology,* **76**(3): 271-278.

Jaquet, N. & H. Whitehead. 1996. Scale-dependent correlation of sperm whale distribution with environmental features and productivity in the South Pacific. *Marine Ecology Progress Series,* **135**(1-3): 1-9.

Johnson, D.F., L.W. Botsford, R.D. Methot Jr., & T.C. Wainwright. 1986. Wind stress and cycles in Dungeness crab (Cancer magister) catch off California, Oregon, and Washington. *Canadian Journal of Fisheries and Aquatic Sciences,* **43**(4): 838-845.

Kaeriyama, M., M. Nakamura, R. Edpalina, J.R. Bower, H. Yamaguchi, R.V. Walker, & K.W. Myers. 2004. Change in feeding ecology and trophic dynamics of Pacific salmon (*Oncorhynchus* spp.) in the central Gulf of Alaska in relation to climate events. *Fisheries Oceanography,* **13**(3): 197-207.

Karagatzides, D. 2006. Nitrogen and phosphate dynamics in an old-growth rainforest: An experimental test of the nutrient retention hypothesis. Ph.D., Queen's University, Kingston, Ontario, Canada.

Keiper, C.A., D.G. Ainley, S.G. Allen, & J.T. Harvey. 2005. Marine mammal occurrence and ocean climate off central California, 1986 to 1994 and 1997 to 1999. *Marine Ecology Progress Series,* **289**: 285-306.

Kim, S.L. & J.S. Oliver. 1989. Swarming benthic crustaceans in the Bering and Chukchi seas and their relation to geographic patterns in gray whale feeding. *Canadian Journal of Zoology,* **67**(6): 1531-1542.

Kinlan, B.P. 2003. Linking environmental forcing, kelp forest habitat dynamics, and community structure in the Northeast Pacific. *Journal of Phycology,* **39**(S1): 29.

Koehl, M.A.R. 1986. Seaweeds in moving water: form and mechanical function. On the economy of plant form and function: Proceedings of the Sixth Maria Moors Symposium, "Evolutionary Constraints on Primary Productivity: Adaptive Patterns of Energy Capture in Plants", Harvard Forest, August 1983 pp. 603-634.

Koehl, M.A.R. & S.A. Wainwright. 1977. Mechanical adaptations of a giant kelp. *Limnology and Oceanography,* **22**(6): 1067-1071.

Lalli, C.M. & T.R. Parsons. 1997. Biological oceanography: an introduction. Butterworth-Heinemann: Woburn, MA, USA. 314 p.

Legendre, P. & L. Legendre. 1998. Numerical ecology: second English edition. Elsevier: Amsterdam, The Netherlands. 853 p.

Littaye, A., A. Gannier, S. Laran, & J.P.F. Wilson. 2004. The relationship between summer aggregation of fin whales and satellite-derived environmental conditions in the northwestern Mediterranean Sea. *Remote Sensing of Environment,* **90**(1): 44-52.

Love, M.S., M.H. Carr, & L.J. Haldorson. 1991. The ecology of substrate-associated juveniles of the genus *Sebastes*. *Environmental Biology of Fishes,* **30**: 657-664.

Mauchline, J. 1980. The biology of mysids and euphausiids. Academic Press: London, England. 680 p.

Maxell, B.A. & K.A. Miller. 1996. Demographic studies of the annual kelps *Nereocystis luetkeana* and *Costaria costata* (Laminariales, Phaeophyta) in Puget Sound, Washington. *Botanica Marina,* **39**(5): 479-489.

McGowan, J.A., S.J. Bograd, R.J. Lynn, & A.J. Miller. 2003. The biological response to the 1977 regime shift in the California Current. *Deep-Sea Research Part II - Topical Studies in Oceanography,* **50**(14-16): 2567-2582.

Miller, A.K. & W.J. Sydeman. 2004. Rockfish response to low-frequency ocean climate change as revealed by the diet of a marine bird over multiple time scales. *Marine Ecology Progress Series,* **281**: 207-216.

Murison, L.D., D.J. Murie, K.R. Morin, and de Silva Curiel, J. 1984. Foraging of the gray whale along the West coast of Vancouver Island, British Columbia. *In* The gray whale *Eschrichtius robustus*. *Edited by* M.L. Jones, S.L. Swartz and S. Leatherwood. Academic Press, Inc., Orlando, FL, USA. pp. 451-463.

Natunewicz, C.C. & C.E. Epifanio. 2001. Spatial and temporal scales of patches of crab larvae in coastal waters. *Marine Ecology Progress Series,* (212): 217-222.

Nerini, M. 1984. A review of gray whale feeding ecology. *In* The gray whale *Eschrichtius robustus*. *Edited by* M.L. Jones, S.L. Swartz and S. Leatherwood. Academic Press, Inc., Orlando, FL, USA. pp. 423-448.

Nicholson, N.L. 1970. Field studies on the giant kelp *Nereocystis*. *Journal of Phycology,* **6**(2): 177-182.

Niemi, A. 1982. Dynamics of phytoplankton in the brackish-water inlet Pojoviken, southern coast of Finland. *Hydrobiologia,* **86**(1-2): 33-39.

North Pacific Marine Science Organisation (PICES). 2005. Report of the study group on fisheries and ecosystem responses to recent regime shifts. No. 28, North Pacific Marine Science Organisation (PICES), Sidney, BC, Canada.

H. M. Patterson. 2004Small-scale distributions and dynamics of the mysid prey of gray whales (*Eschrichtius robustus*) in Clayoquot Sound, British Columbia, Canada. M.Sc., University of Victoria. Victoria, BC Canada.

Petrell, R.J., K. Mazhari Tabrizi, P.J. Harrison, & L.D. Druehl. 1993. Mathematical model of *Laminaria* production near a British Columbian salmon sea cage farm. *Journal of Applied Phycology,* **5**(1): 1-14.

Powell, T.M. 1989. Physical and biological scales of variability on lakes, estuaries and the coastal ocean. *In* Perspectives in ecological theory. *Edited by* J. Roughgarden, R.M. May and S.A. Levin. Princeton University Press, Princeton, NJ, USA. pp. 157-176.

Pyper, B.J. & R.M. Peterman. 1998. Comparison of methods to account for autocorrelation in correlation analyses of fish data. *Canadian Journal of Fisheries and Aquatic Sciences,* **55**(9): 2127-2140.

Roman, M.R. 1978. Tidal resuspension in Buzzards Bay, Massachusetts. 2. Seasonal changes in the size distribution of chlorophyll, particle concentration, carbon and nitrogen in resuspended particulate matter. *Estuarine and Coastal Marine Science,* **6**(1): 47-53.

Ryan, J.P., F.P. Chavez, & J.G. Bellingham. 2005. Physical-biological coupling in Monterey Bay, California: topographic influences on phytoplankton ecology. *Marine Ecology Progress Series,* **287**: 23-32.

Schabes, M. & W. Hamner. 1992. Mysid locomotion and feeding kinematics and water-flow patterns of Antarctomysis-Sp *Acanthomysis-Sculpta* and *Neomysis rayii*. *Journal of Crustacean Biology,* **12**(1): 1-10.

Shaffer, J.A. 2000. Seasonal variation in understory kelp bed habitats of the Strait of Juan de Fuca. *Journal of Coastal Research,* **16**(3): 768-775.

Shields, T. 1988. The potential and feasibility of *Macrocystis* aquaculture in Alaska. Proceedings of the fourth Alaska Aquaculture Conference, Sitka, AK (USA),18-21 Nov 1987 **Vol. 4,** pp. 19-25.

Singer, M.M. 1985. Food habits of juvenile rockfishes (*Sebastes*) in a central California kelp forest. *Fishery Bulletin,* **83**(4): 531-542.

Smith, B.D. & F.E. Foreman. 1984. An assessment of seaweed decomposition within a southern Strait of Georgia seaweed community. *Marine Biology,* **84**(2): 197-205.

Steele, J.H. 1989. Discussion: scale and coupling in ecological systems. *In* Perspectives in ecological theory. *Edited by* J. Roughgarden, R.M. May and S.A. Levin. Princeton University Press, Princeton, NJ, USA. pp. 177-180.

Stelle, L.L. 2001. Behavioural ecology of summer resident gray whales (*Eschrichtius robustus*) feeding on mysids in British Columbia, Canada. Ph.D., University of California, Los Angeles. Los Angeles, California, USA.

Sydeman, W.J. & S.G. Allen. 1999. Pinniped population dynamics in central California: Correlations with sea surface temperature and upwelling indices. *Marine Mammal Science,* **15**(2): 446-461.

Tabachnick, B.G. & L.S. Fidell. 1983. Using multivariate statistics. Harper & Row: New York, NY, USA. 509 p.

Takahashi, K. 2004. Feeding ecology of mysids in freshwater and coastal marine habitats: A review. *Bulletin of Plankton Society of Japan,* **51**(1): 46-72.

Takahashi, K., T. Hirose, & K. Kawaguchi. 1999. The importance of intertidal sand-burrowing peracarid crustaceans as prey for fish in the surf-zone of a sandy beach in Otsuchi Bay, northeastern Japan. *Fisheries Science,* **65**(6): 856-864.

Thomson, R.E. 1981. Oceanography of the British Columbia Coast. No. 56, Department of Fisheries and Oceans, Ottawa, Canada. 291 p.

Turpen, S., J.W. Hunt, B.S. Anderson, & J.S. Pearse. 1994. Population structure, growth, and fecundity of the kelp forest mysid *Holmesimysis costata* in Monterey Bay, California. *Journal of Crustacean Biology,* **14**(4): 657-664.

West, T.L., D.R. Corbett, L.M. Clough, M.W. Calfee, & J.E. Frank. 2005. Impacts of trawling and wind disturbance on water column processes in the Pamlico River Estuary, North Carolina.

Yen, P.P.W., W.J. Sydeman, K.H. Morgan, & F.A. Whitney. 2005. Top predator distribution and abundance across the eastern Gulf of Alaska: Temporal variability and ocean habitat associations. *Deep-Sea Research Part II - Topical Studies in Oceanography,* **52**(5-6): 799-822.

Chapter 3 – Conclusions

In order to evaluate the effectiveness of this research and contribution of the research results to a general understanding of the factors influencing gray whale abundance, it is necessary to review the research questions and objectives of this project.

Objectives and research questions

There were several research questions for this research set out in Chapter 1:

1. What role do environmental variables play in influencing the relative abundance of gray whales in the study area?
2. Can these environmental variables, or forcing factors, be used to predict future gray whale abundance?
3. Are time lags present in the relationship between forcing and forced parts of the food web and if present, how long are they?
4. To what extent do the data environmental data collected at a broad spatial scale predict gray whale data collected at a fine spatial scale?

These research questions were addressed through the use of single and multiple regression analyses to test for relationships between gray whale abundance and environmental variables.

Mathematical model effectiveness

The first objective and research question involves investigating whether or not relationships exist between gray whale abundance and environmental variables, and if such relationships exist, how strong are they? To address this question/objective, several steps were taken. First, candidate environmental variables were selected and aggregated at four time scales: weekly, semi-monthly, monthly and annually. Second, single regressions were performed on each independent variable, with gray whale abundance as the dependent variable. Third, those independent variables which met pre-set criteria in terms of R^2 and p values were entered into multiple models in different combinations, and the amount of variance explained was evaluated. The second objective was to examine the time scales over

which gray whales might respond to environmental forcing. This was tested through the use of lagged variables, that is to say including data from previous periods in regression models to test their explanatory power.

Model explanatory power increased as temporal scales also increased in length. It was not possible to create a multiple model at the weekly scale due to a lack of suitable variables. At the semi-monthly scale, the best model explained only 19.2% of the variance ($p=0.005$), and was composed of two independent variables, SST at Nootka, and wind speed La Perouse Bank lagged 3 periods. The best model using data aggregated at a monthly scale explained only 37.4% of the variance ($p=0.012$). This model included five independent variables: SST at Nootka, wind speed at La Perouse Bank lagged 2 months, sunlight at Tofino, sunlight at Tofino lagged 12 months, and Month = July.

The model with the most explanatory power was created using data aggregated at the annual temporal scale. This model was composed of two independent variables, wind speed at La Perouse and upwelling at 48ºN lagged 2 years. These two variables combined to create a model that explained 89.6% of the variance ($p=0.004$). This model combined data from the same year (gray whale abundance and wind speed) and time-lagged data (lag 2 years upwelling at 48ºN).

Thus, the first two objectives of this study were met through the use of regression analysis to examine relationships between gray whale abundance and environmental variables, and the time scales over which gray whales respond were examined through the use of time-lagged variables.

Variables influencing localised gray whale abundance and methods by which these variables may affect gray whale abundance

The results presented here indicate that gray whale abundance in the study area is related to several environmental variables at several different time scales. The strongest relationship was noted at an annual time scale, with two independent variables, wind speed at La Perouse Bank and upwelling at 48ºN lagged 2 years, explaining about 90% of the variance.

There are several pathways through which gray whale abundance could be affected by wind speed at La Perouse Bank and upwelling at 48ºN lagged 2 years, the environmental

variables included in the best model. Mysids are expected to feed on phytoplankton, small zooplankton, kelp or detritus, depending on the time of year and what prey are most available (Mauchline 1980, Duggins *et al.* 1989, Schabes & Hamner 1992, Turpen *et al.* 1994). Fluctuations in primary productivity may affect mysid production (Stelle 2001), which could be experienced through any of the above pathways, as all are influenced directly or indirectly by environmental variables which are themselves related to primary productivity. In particular, wind speed is negatively correlated with gray whale abundance, meaning that as wind speed increases, gray whale abundance decreases. This may be related to both the potential phytoplankton and kelp pathways in that greater wind speeds are expected to detach more kelp, and mix more phytoplankton out of the euphotic zone, resulting in a negative relationship between wind speed and these factors. It is not immediately apparent how upwelling at 48ºN lagged 2 years is related to gray whale abundance; it is expected that most production of phytoplankton, zooplankton and kelp would be reliant upon upwelling occurring at shorter time scales. However, if the mysids are overwintering for multiple years, then it there is the potential for upwelling lagged two years to be important over their life cycle.

It is unlikely that top-down pressures from gray whale predation have a strong effect from one year to another. Gray whale abundance was highly related to previous periods at all scales but the annual scale, pointing to a seasonal effect of gray whale abundance, rather than one highly related at an annual scale. Also, the correlation between all related periods was positive at all time scales, further supporting the idea of gray whale abundance being seasonal.

Time periods were included in the initial single regressions to test if any time period was more related to gray whale abundance. The only time period that was related to gray whale abundance was identified at the monthly scale, this variable was the month of July, which explained 16.6% of the variance ($p=0.014$). This may indicate that some event is occurring during July which is related to gray whale abundance; unfortunately there is no way to identify the actual event. Overall, the effects of time period were negligible.

Time lags

Another of the research questions/objectives focused on the identification of time lags between environmental variables and gray whale abundance. To test for their presence, all data at all temporal scales were lagged at 1, 2, 3 periods and 1 year, except the annual data, which were only lagged 1 and 2 years due to a short data series. Time lags did not appear to be as prevalent as expected. That said, regression analysis is not an ideal tool for the identification of time lags. The only variables identified exhibiting time lags which were at the semi-monthly scale: s wind speed at La Perouse Bank lagged 3 periods; the monthly scale: wind speed at La Perouse Bank lagged 2 months, and sunlight at Tofino lagged 12 months; and at the annual scale: upwelling at 48ºN lagged 2 years. The best model included the latter variable. However, few time lags were apparent at shorter time scales, where I had expected them to be important in terms of plankton dynamics; for example to track the effects of the spring bloom over the early summer.

Further research is necessary to identify other time lags, as the presence of lags at time scales other than those examined here is possible. The use of other statistical methods better suited to identifying time lags, such as time series analysis or cross correlation analysis, would likely be more effective in identifying time lags and lags of variable length.

Scale and scale coupling

The final research question/objective concerns the presence of the concept of scale coupling. This research revealed that scale coupling was present, although it was dependent on the temporal scale at which the data were examined. Model effectiveness increased with temporal scale, in that models created at shorter time scales had lower explanatory power than those created at longer time scales, and thus coupling only occurred at longer time scales. The most explanatory model was created at an annual temporal scale, and thus the best coupling between these data was also observed at this scale. Thus, as variability decreased due to data being aggregated over broader time periods, the strength of the relationships between variables increased and scale coupling was present.

Similarities to other research

This research has shown several similarities, though general ones, with other marine research involving the effects of environmental variables on organisms. In this research, a

relationship was identified between gray whale abundance and environmental variables, as has been noted for other marine mammals, though over broader spatial scales (Jaquet & Whitehead 1996, Benson *et al.* 2002, Littaye *et al.* 2004, Keiper *et al.* 2005). Research by Keiper *et al.* (2005) also found a negative relationship between wind speed and marine mammal abundance off California, and it is possible that the pathway(s) by which marine mammals are affected by wind speed are the same as in this study. However, those pathways remain unknown at present.

In terms of the effects of environmental forcing factors on mysids, Stelle (2001) noted that mysid abundance may be related to primary productivity and thus to the abundance of kelp and/or phytoplankton. These are the same pathways that I have identified in this research as possible pathways for the environmental variables to affect gray whale abundance, but at present this pathway remains speculative.

Summary

The effectiveness of regression models at relating environmental variables and gray whale abundance increased with temporal scale. The most explanatory multiple regression model was created with data aggregated at an annual time scale, explaining 89.6% of the variance ($p=0.004$). The two independent variables in this model are wind speed at La Perouse Bank and upwelling at 48ºN lagged 2 years. These variables have the ability to alter primary production and thus influencing populations and thus gray whale abundance through several pathways, including mysids feeding on phytoplankton, small zooplankton, detritus, or kelp. Both kelp and phytoplankton would be negatively affected by increases in wind speed, with kelp being more likely to be detached in periods of greater wind speed and phytoplankton being more likely to be mixed out of the euphotic layer during periods of increased wind speeds. Thus, it appears that gray whale abundance may be influenced by environmental variables to an extent where annual abundance is altered.

Literature Cited

Benson, S.R., D.A. Croll, B.B. Marinovic, F.P. Chavez, & J.T. Harvey. 2002. Changes in the cetacean assemblage of a coastal upwelling ecosystem during El Nino 1997-98 and La Nina 1999. *Progress in Oceanography,* **54**(1-4): 279-291.

Duggins, D.O., C.A. Simenstad, & J.A. Estes. 1989. Magnification of secondary production by kelp detritus in coastal marine ecosystems. *Science,* **245**(4914): 170-173.

Jaquet, N. & H. Whitehead. 1996. Scale-dependent correlation of sperm whale distribution with environmental features and productivity in the South Pacific. *Marine Ecology Progress Series,* **135**(1-3): 1-9.

Keiper, C.A., D.G. Ainley, S.G. Allen, & J.T. Harvey. 2005. Marine mammal occurrence and ocean climate off central California, 1986 to 1994 and 1997 to 1999. *Marine Ecology Progress Series,* **289**: 285-306.

Littaye, A., A. Gannier, S. Laran, & J.P.F. Wilson. 2004. The relationship between summer aggregation of fin whales and satellite-derived environmental conditions in the northwestern Mediterranean Sea. *Remote Sensing of Environment,* **90**(1): 44-52.

Mauchline, J. 1980. The biology of mysids and euphausiids. Academic Press: London, England. 680 p.

Schabes, M. & W. Hamner. 1992. Mysid locomotion and feeding kinematics and water-flow patterns of Antarctomysis-Sp *Acanthomysis-Sculpta* and *Neomysis rayii*. *Journal of Crustacean Biology,* **12**(1): 1-10.

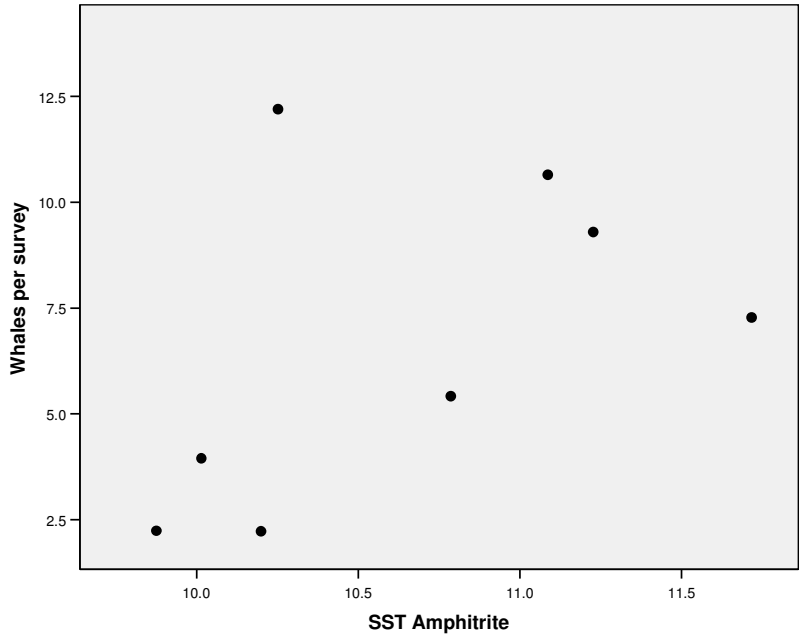
Stelle, L. L. 2001. Behavioural ecology of summer resident gray whales (*Eschrichtius robustus*) feeding on mysids in British Columbia, Canada. Ph.D. Dissertation, University of California, Los Angeles. Los Angeles, California, USA.

Turpen, S., J.W. Hunt, B.S. Anderson, & J.S. Pearse. 1994. Population structure, growth, and fecundity of the kelp forest mysid *Holmesimysis costata* in Monterey Bay, California. *Journal of Crustacean Biology,* **14**(4): 657-664.

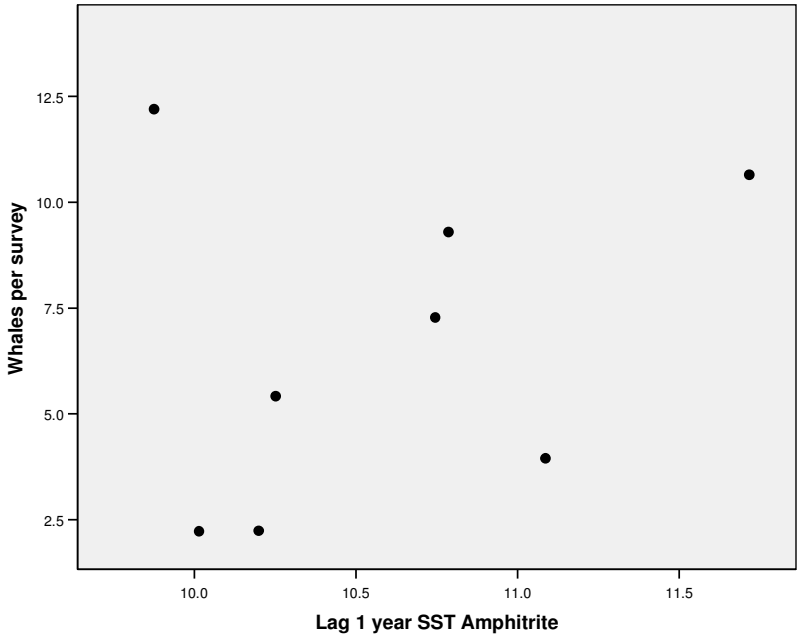
Appendix I. Scatterplots.

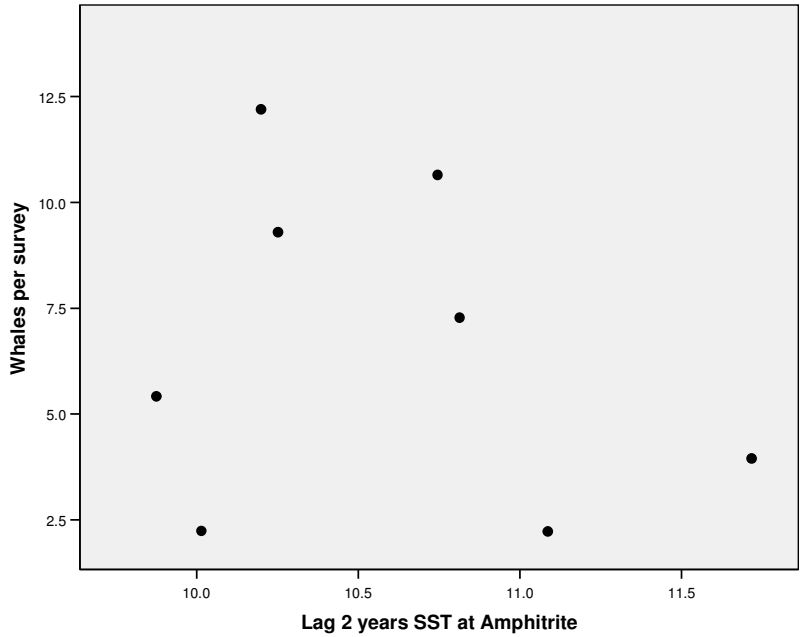
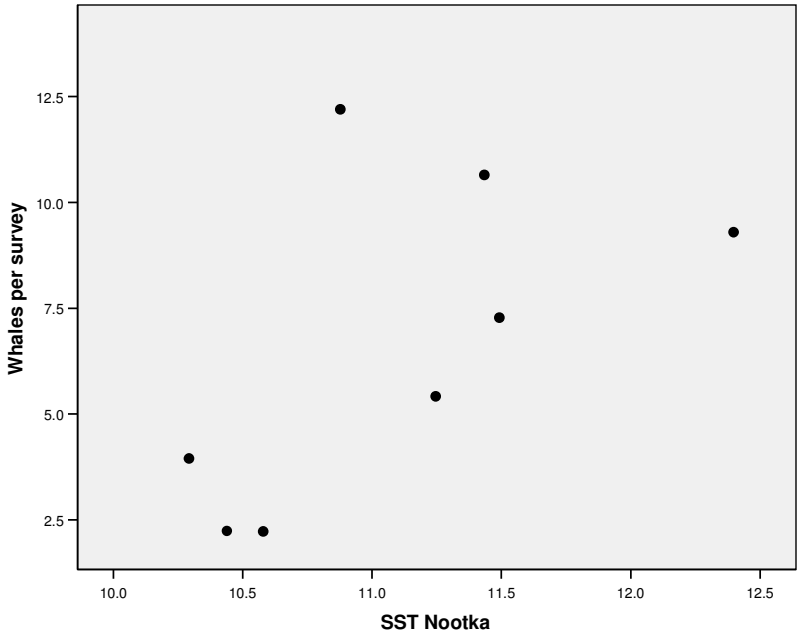
Figure 4. Scatterplots – yearly scale

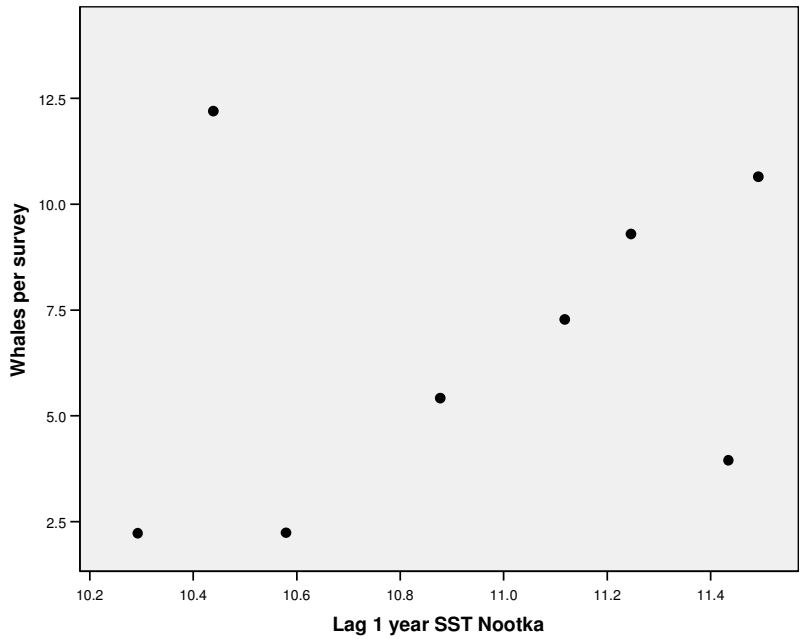
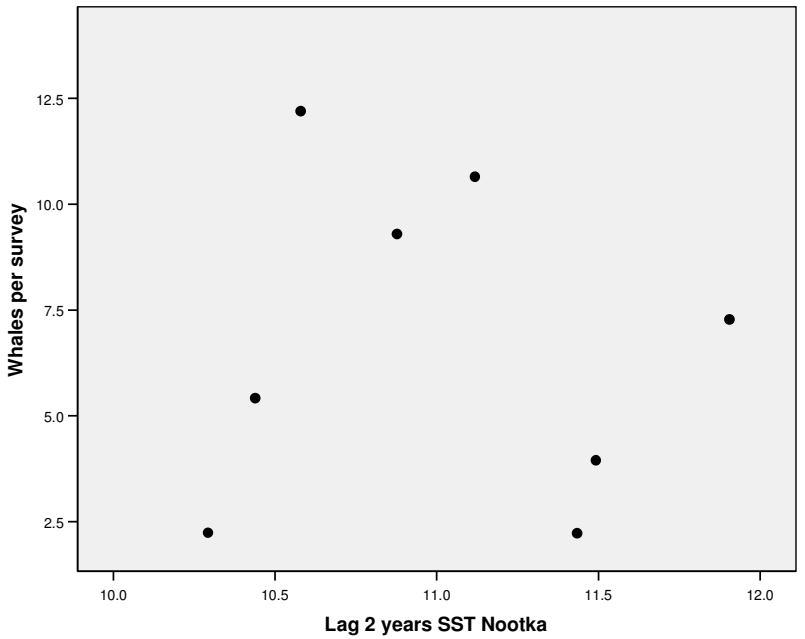
SST Amphitrite vs. whales per survey

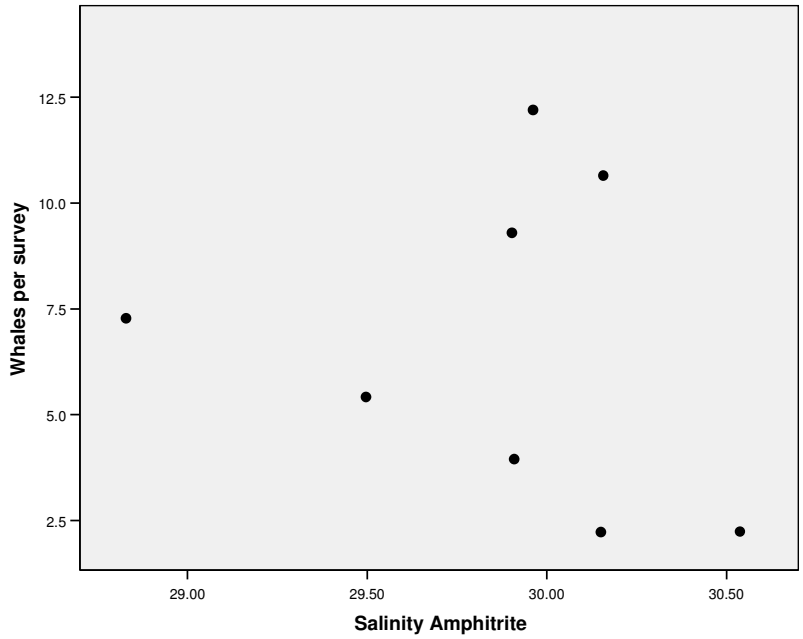
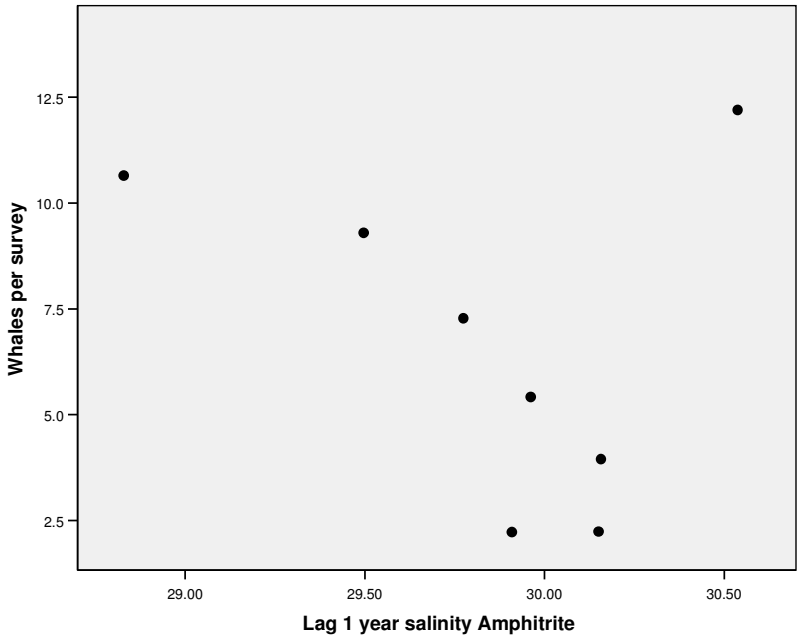


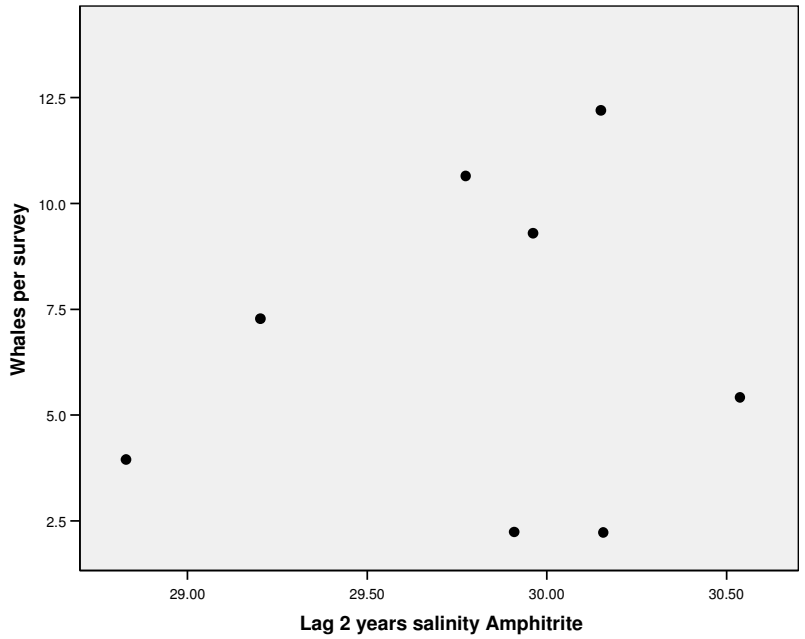
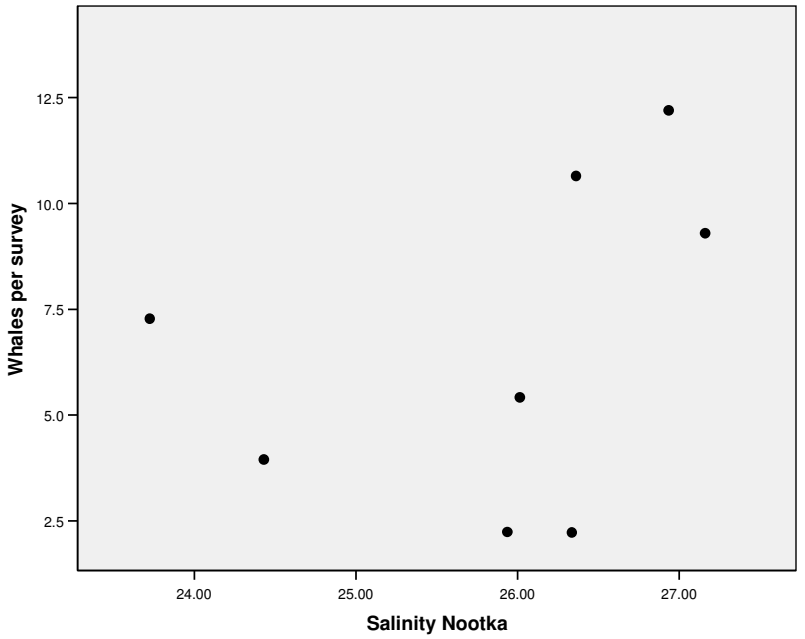
Lag 1 year SST Amphitrite vs. whales per survey



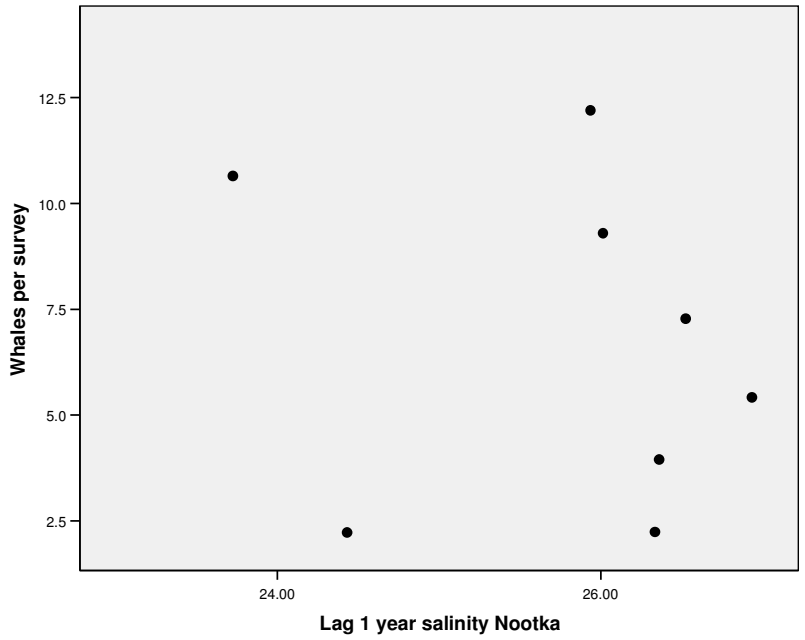
Lag 2 years SST Amphitrite vs. whales per survey	SST Nootka vs. whales per survey
	

Lag 1 year SST Nootka vs. whales per survey	Lag 2 years SST Nootka vs. whales per survey
	

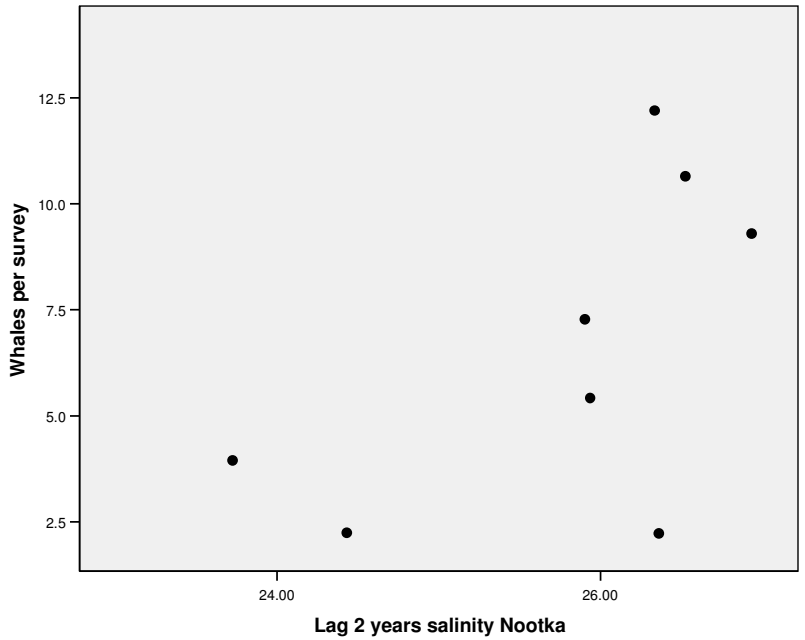
Salinity Amphitrite vs. whales per survey	Lag 1 year salinity Amphitrite vs. whales per survey
	

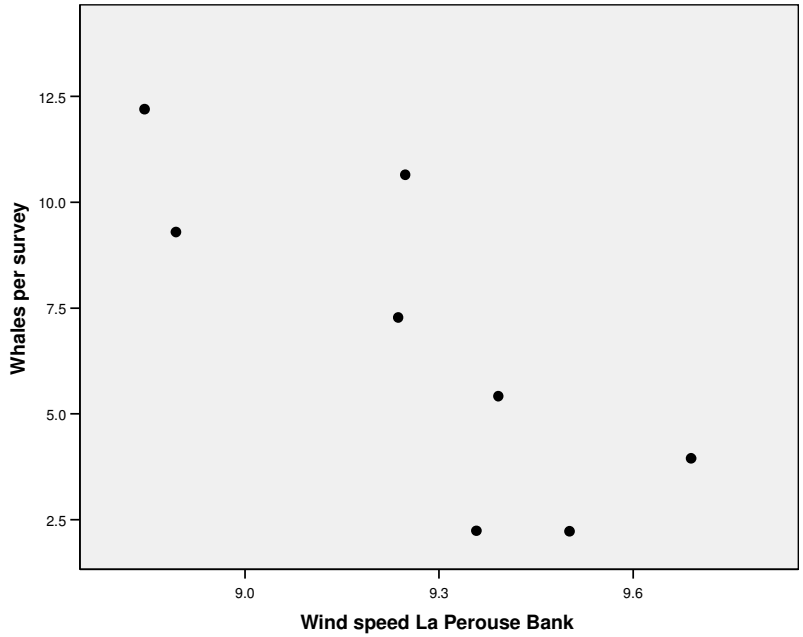
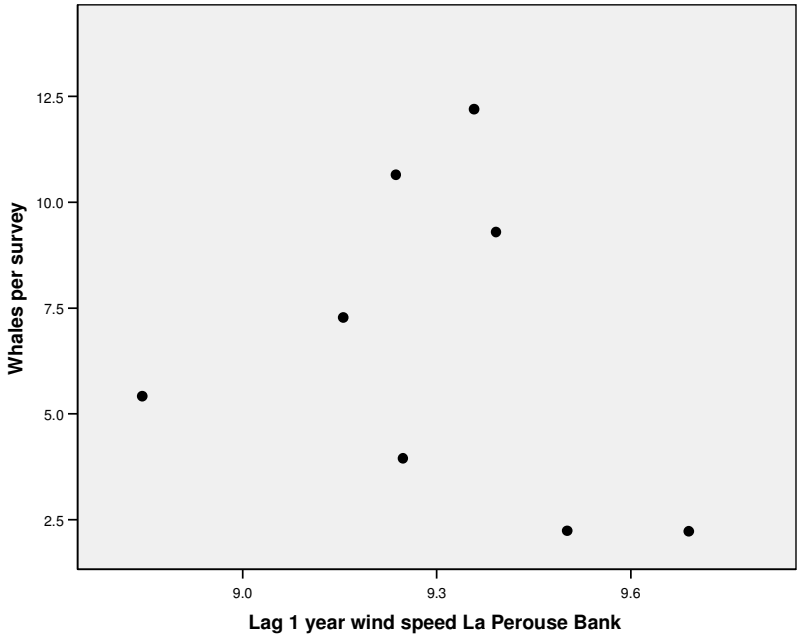
Lag 2 years salinity Amphitrite vs. whales per survey	Salinity Nootka vs. whales per survey
	

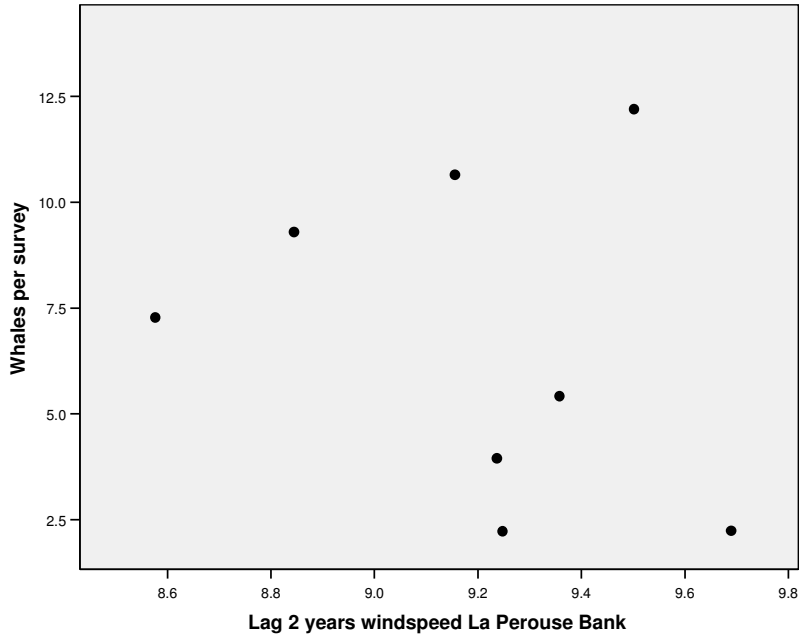
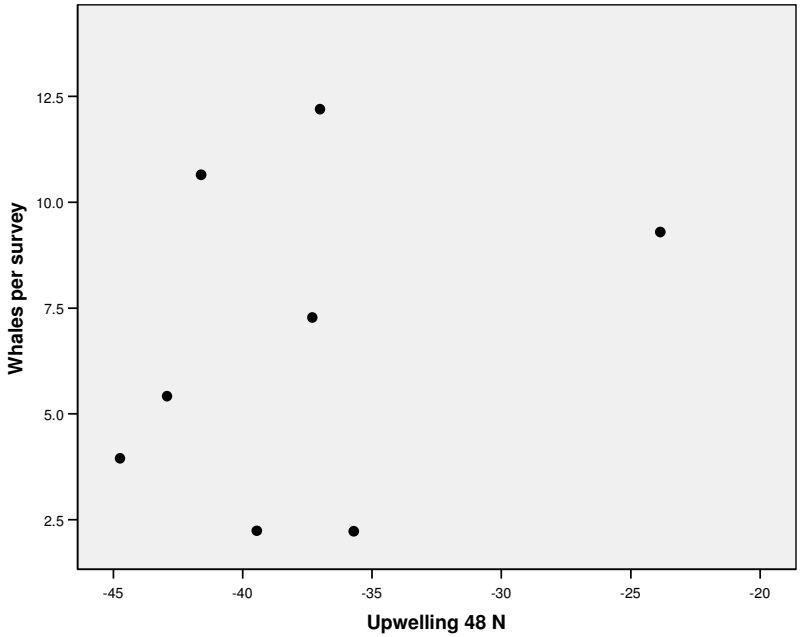
Lag 1 year salinity Nootka vs. whales per survey

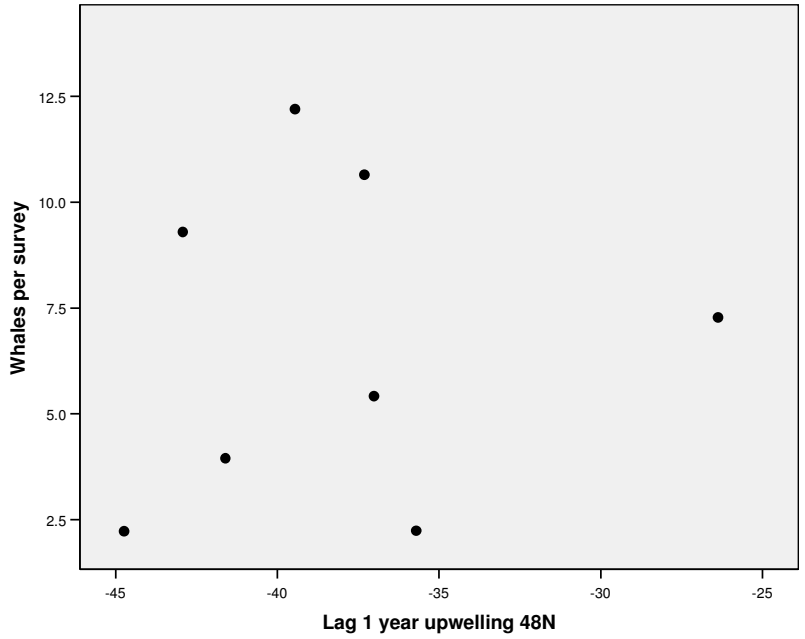
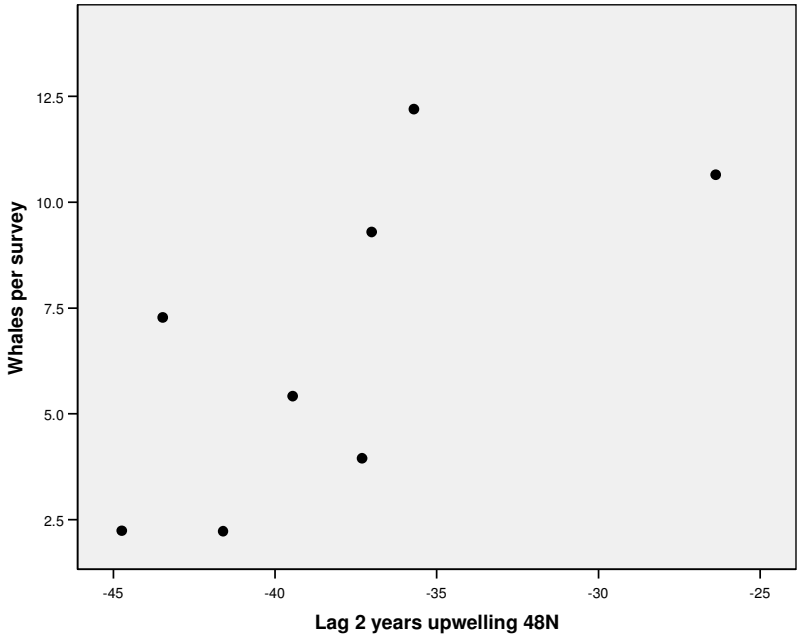


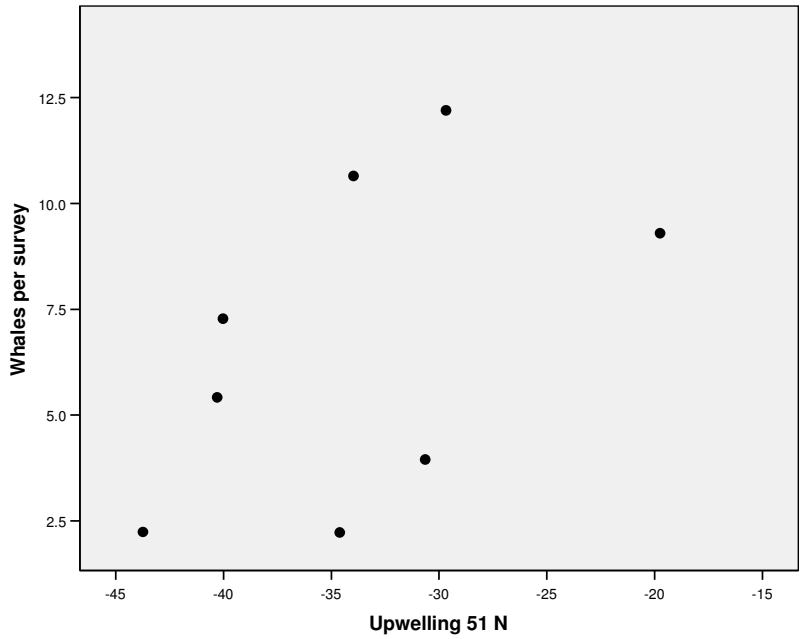
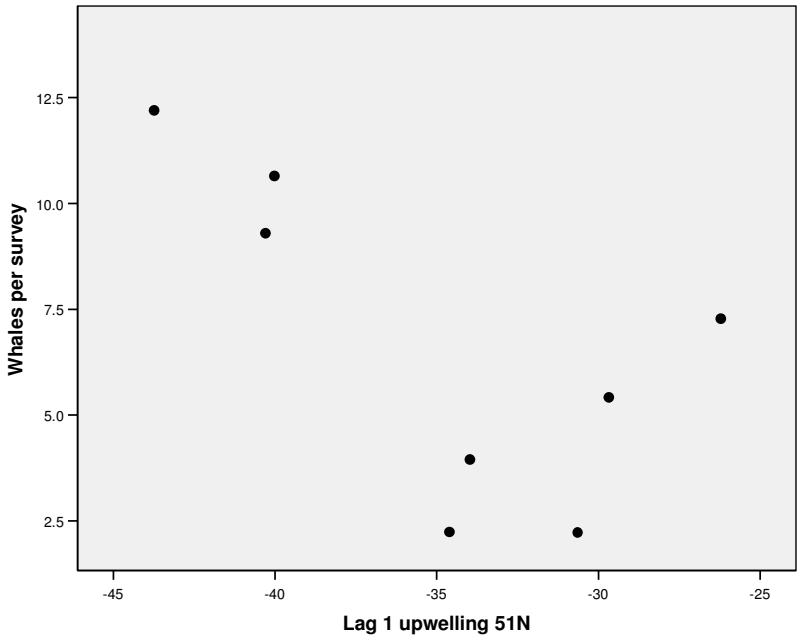
Lag 2 years salinity Nootka vs. whales per survey

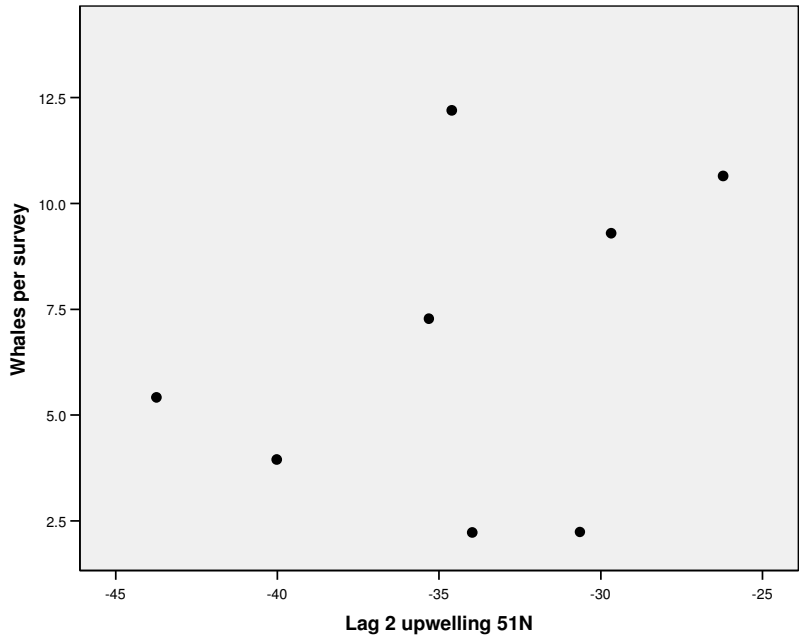
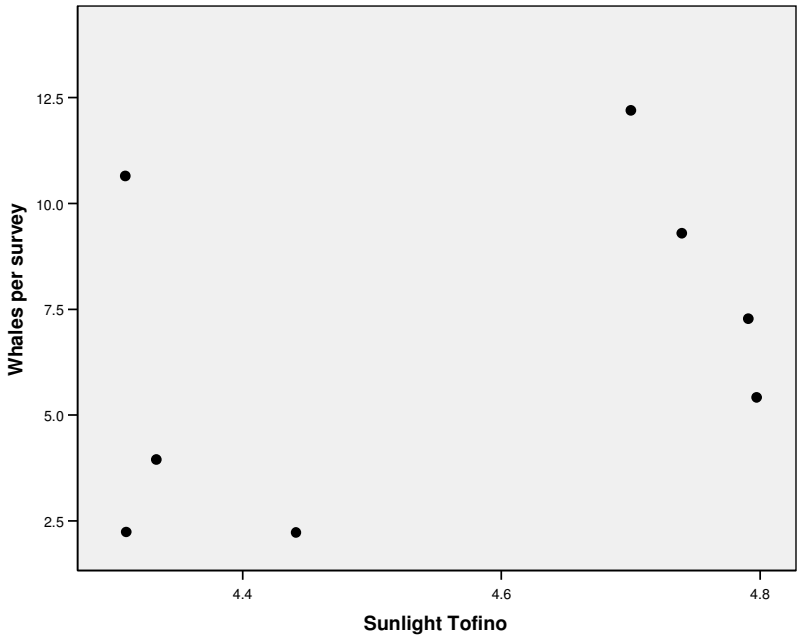


Wind speed La Perouse Bank vs. whales per survey	Lag 1 year wind speed La Perouse Bank vs. whales per survey
	

Lag 2 years wind speed La Perouse Bank vs. whales per survey	Upwelling 48N vs. whales per survey
	

Lag 1 year upwelling 48N vs. whales per survey	Lag 2 years upwelling 48N vs. whales per survey
	

Upwelling 51N vs. whales per survey	Lag 1 year upwelling 51N vs. whales per survey
	

Lag 2 years upwelling 51N vs. whales per survey	Sunlight Tofino vs. whales per survey
	

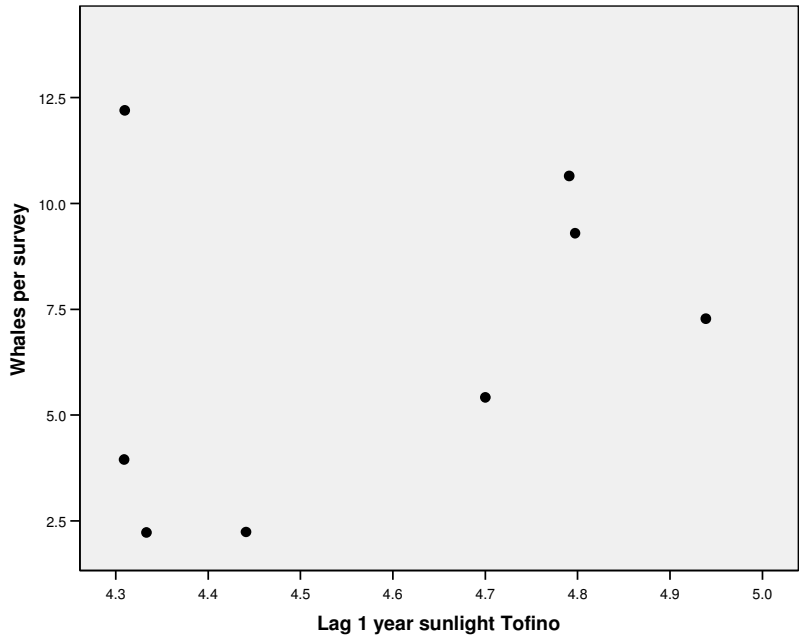
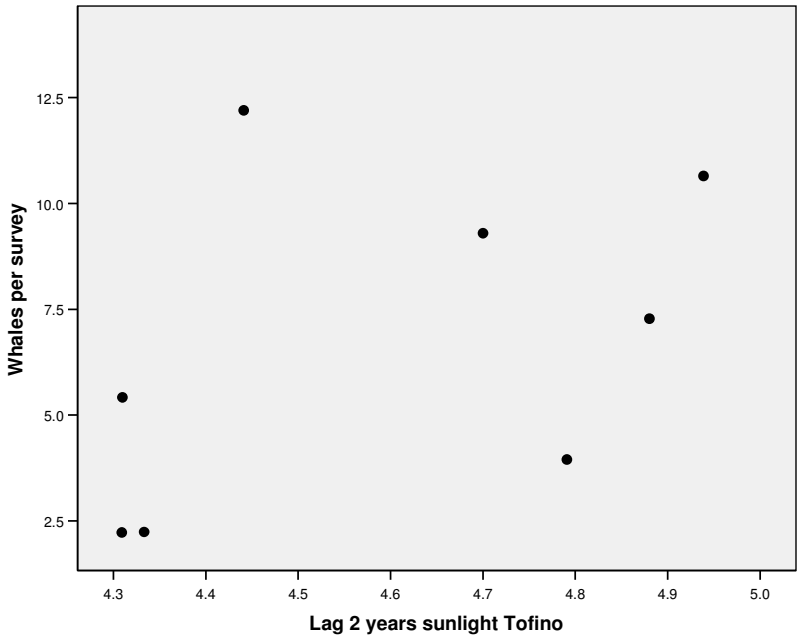
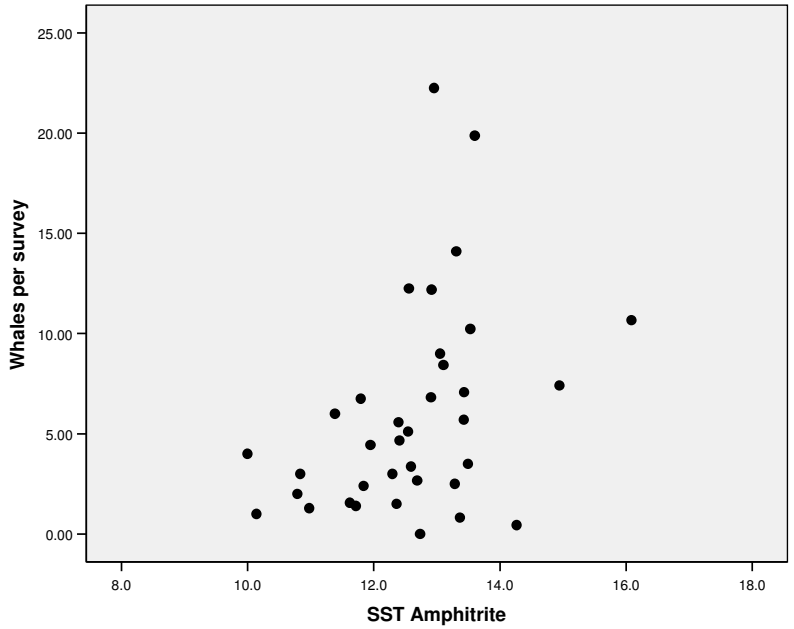
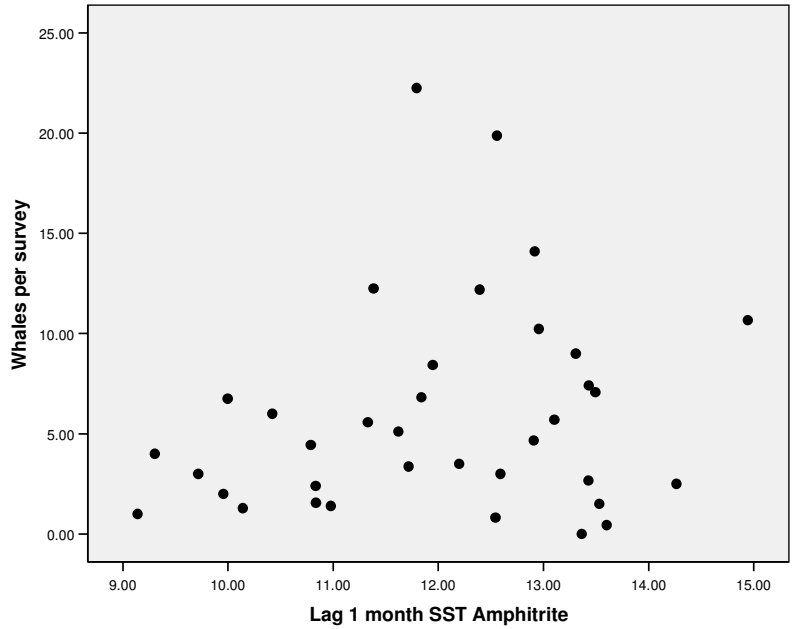
Lag 1 year sunlight Tofino vs. whales per survey	Lag 2 years sunlight Tofino vs. whales per survey
	

Figure 5. Scatterplots – monthly scale.

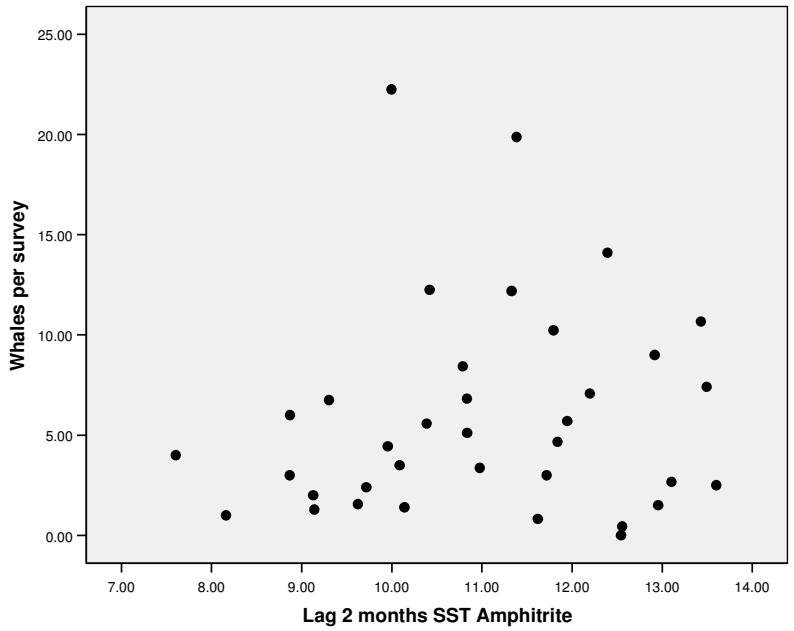
SST Amphitrite vs. whales per survey



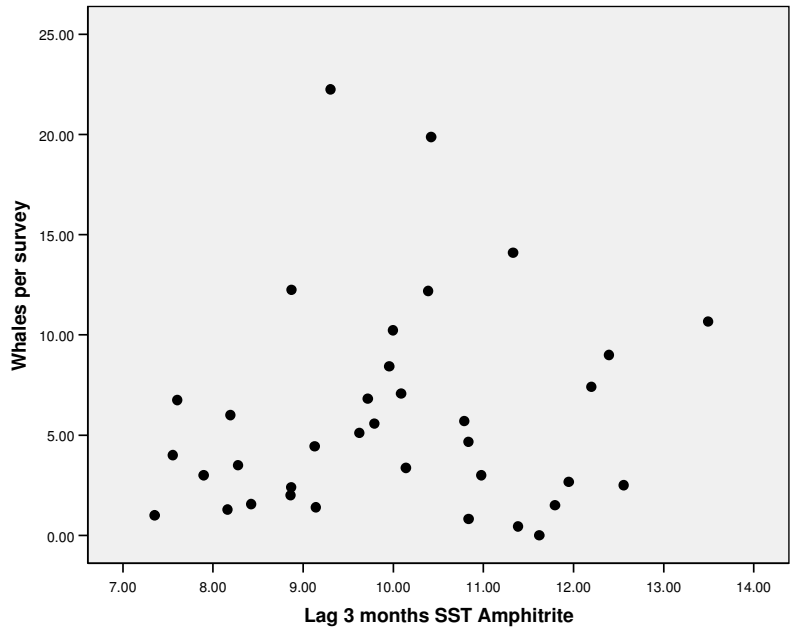
Lag 1 month SST Amphitrite vs. whales per survey



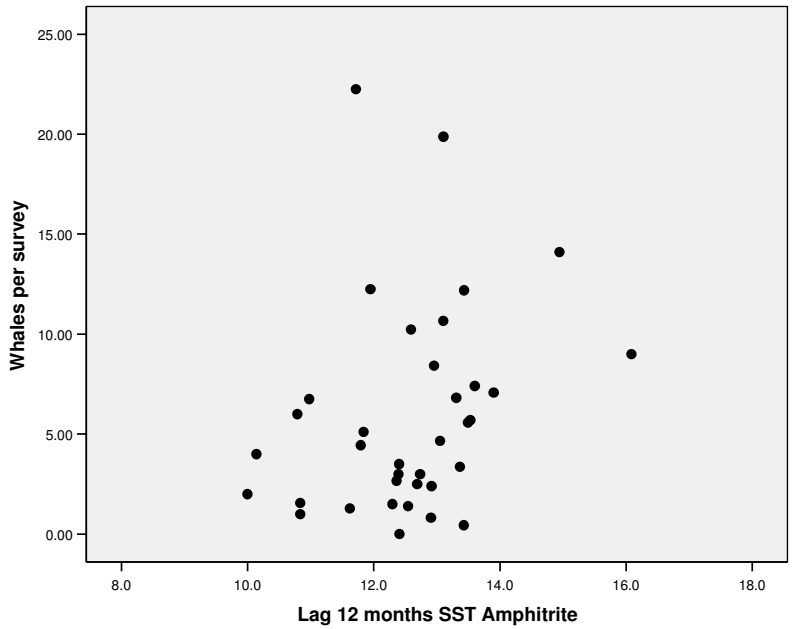
Lag 2 months SST Amphitrite vs. whales per survey



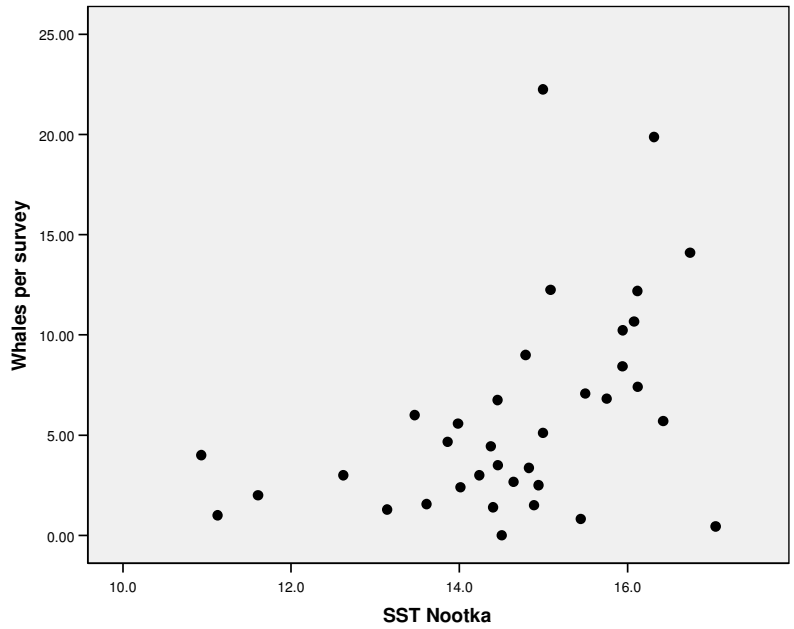
Lag 3 months SST Amphitrite vs. whales per survey



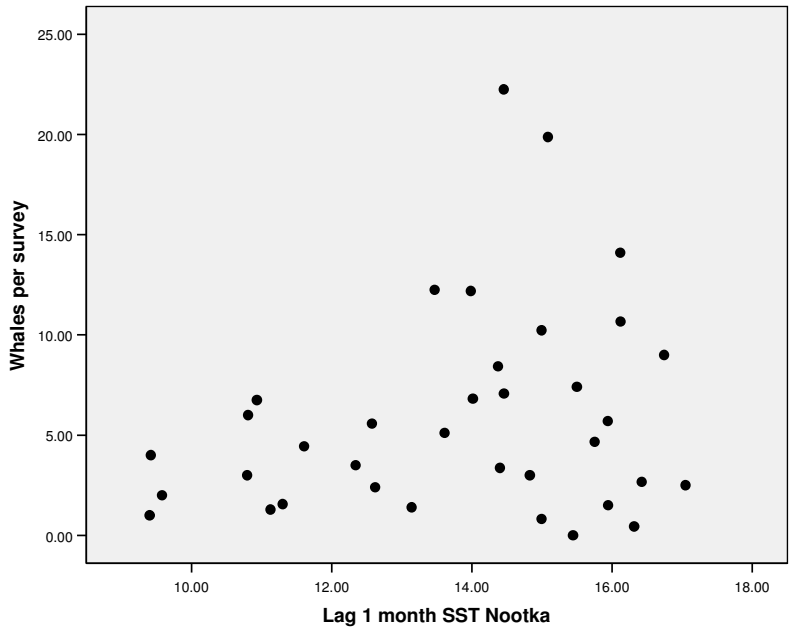
Lag 12 months SST Amphitrite vs. whales per survey



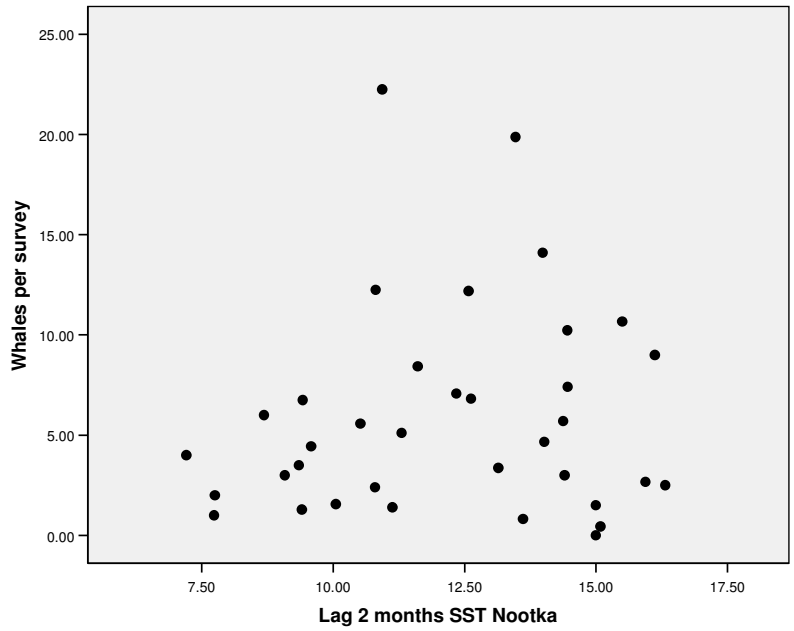
SST Nootka vs. whales per survey



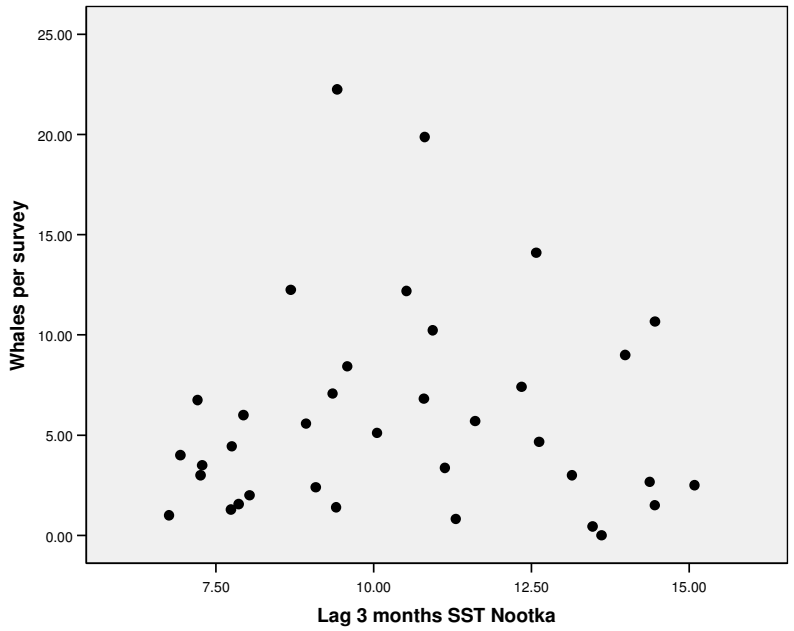
Lag 1 month SST Nootka vs. whales per survey



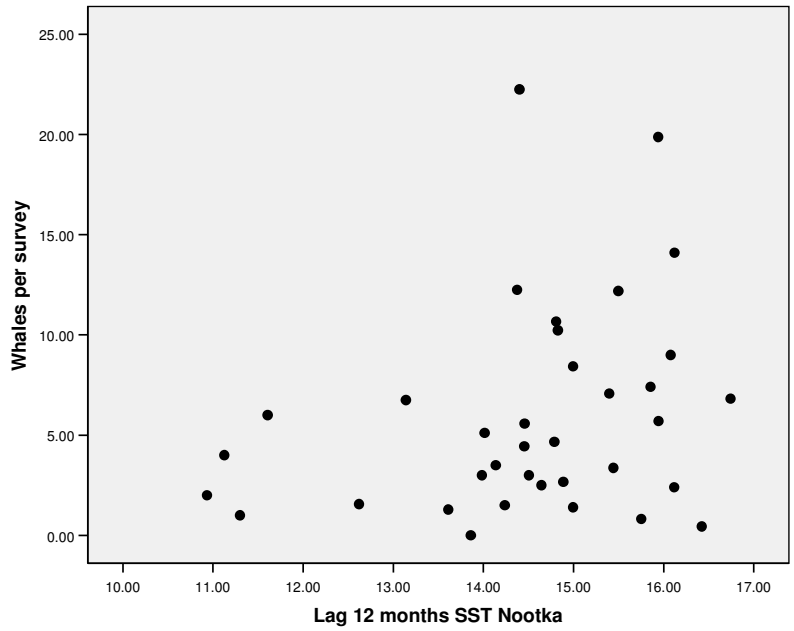
Lag 2 months SST Nootka vs. whales per survey



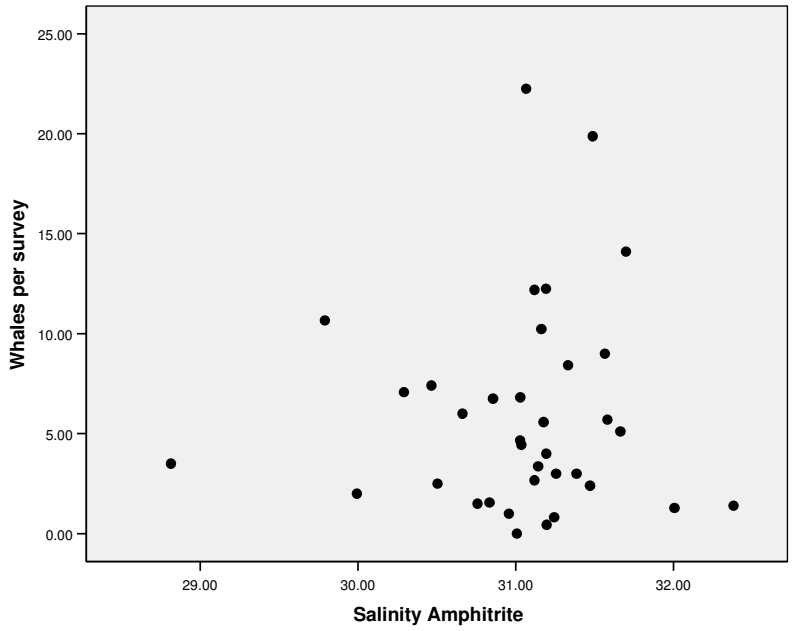
Lag 3 months SST Nootka vs. whales per survey



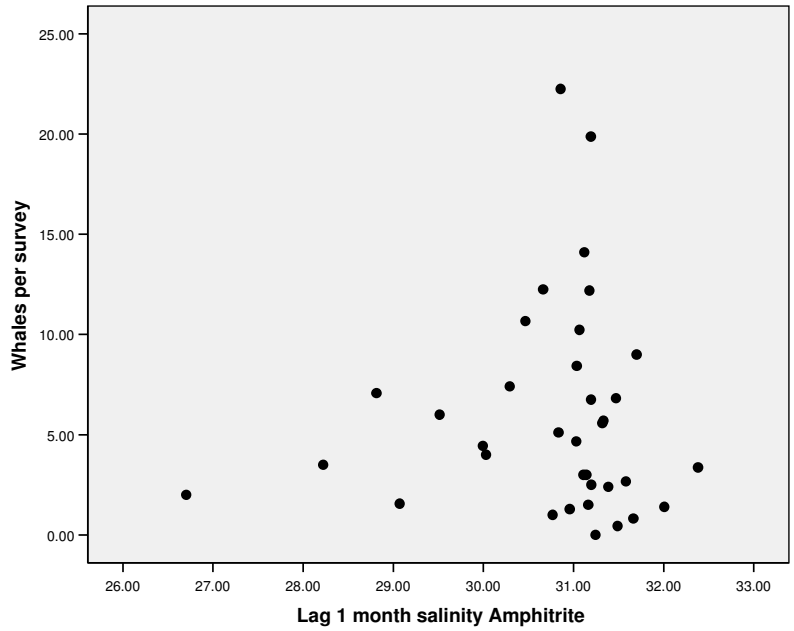
Lag 12 months SST Nootka vs. whales per survey

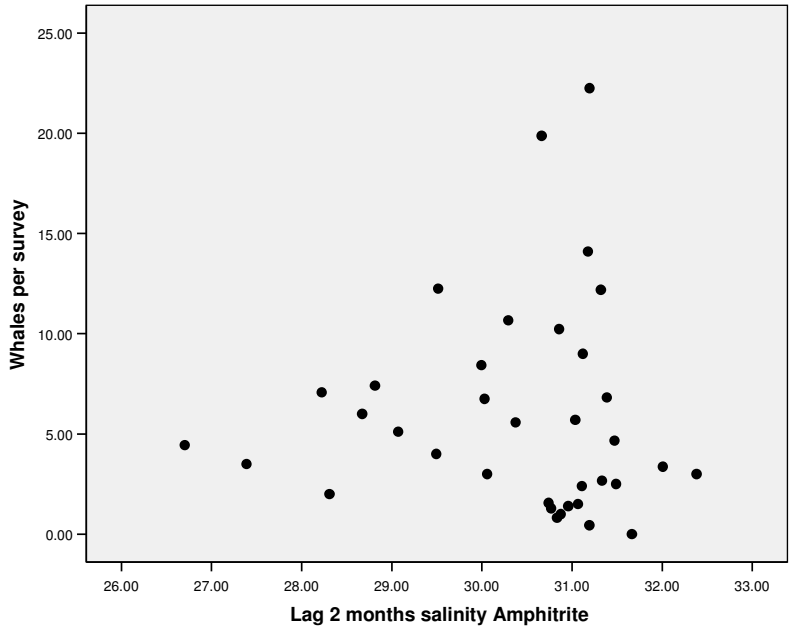
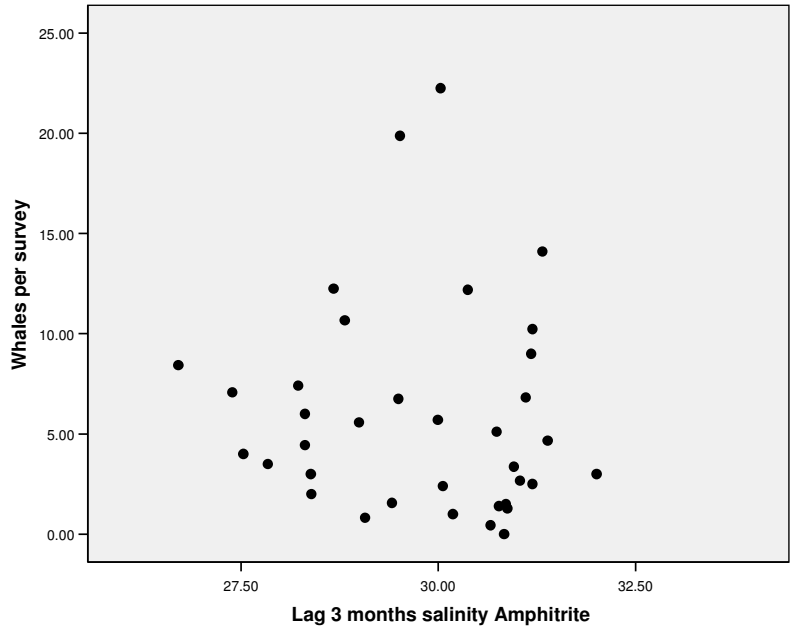


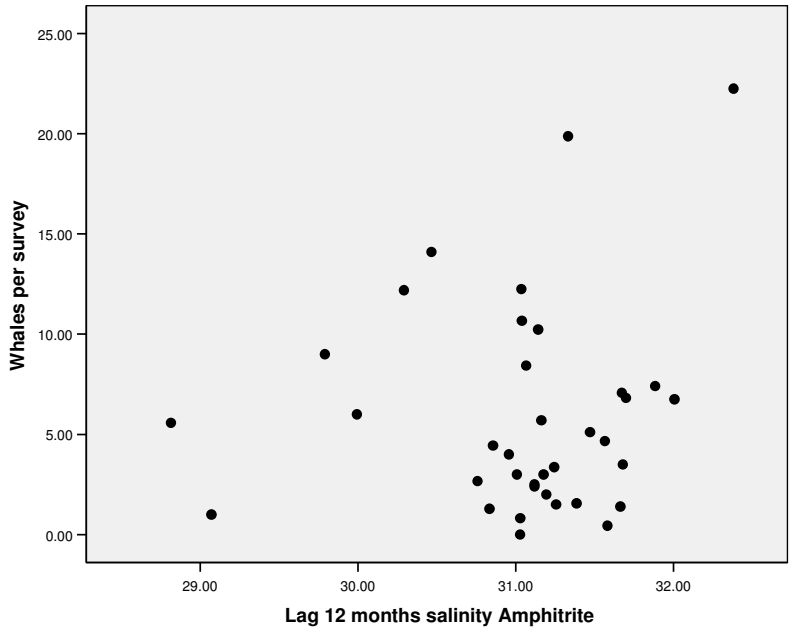
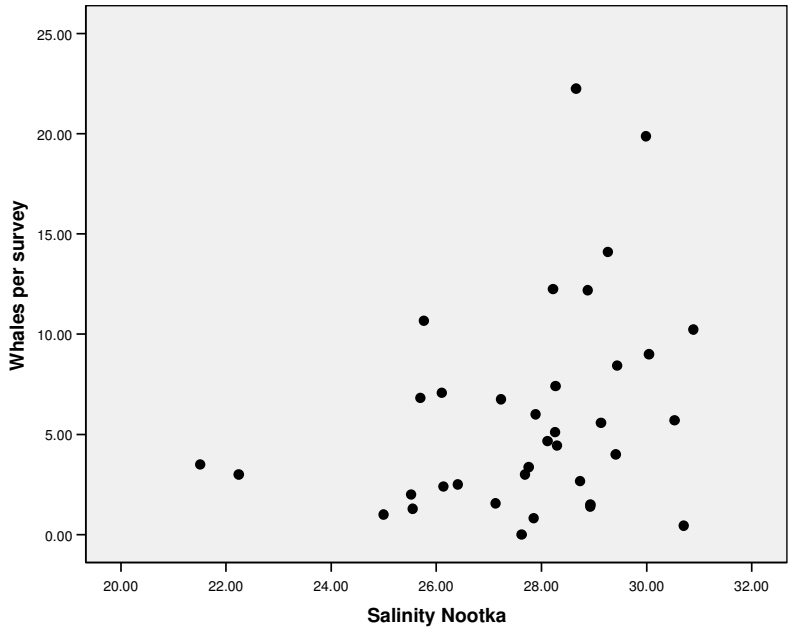
Salinity Amphitrite vs. whales per survey



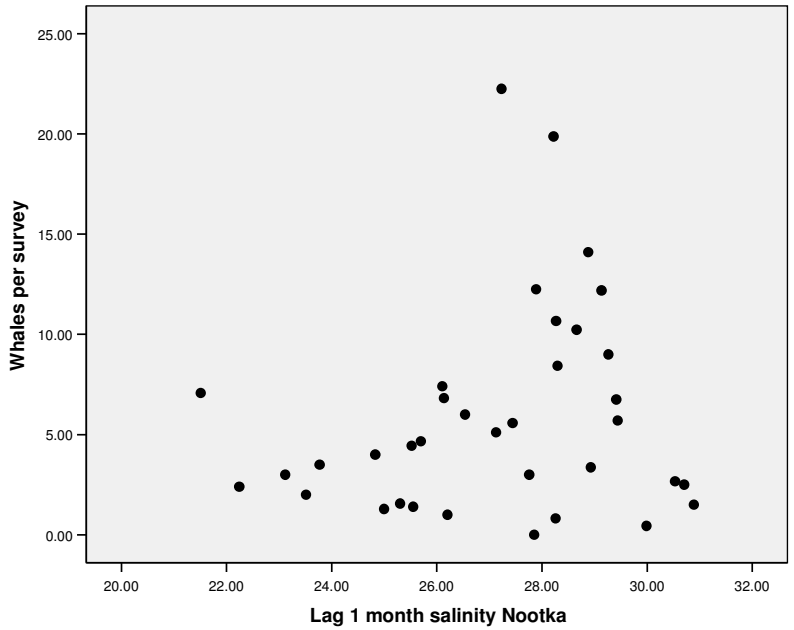
Lag 1 month salinity Amphitrite vs. whales per survey



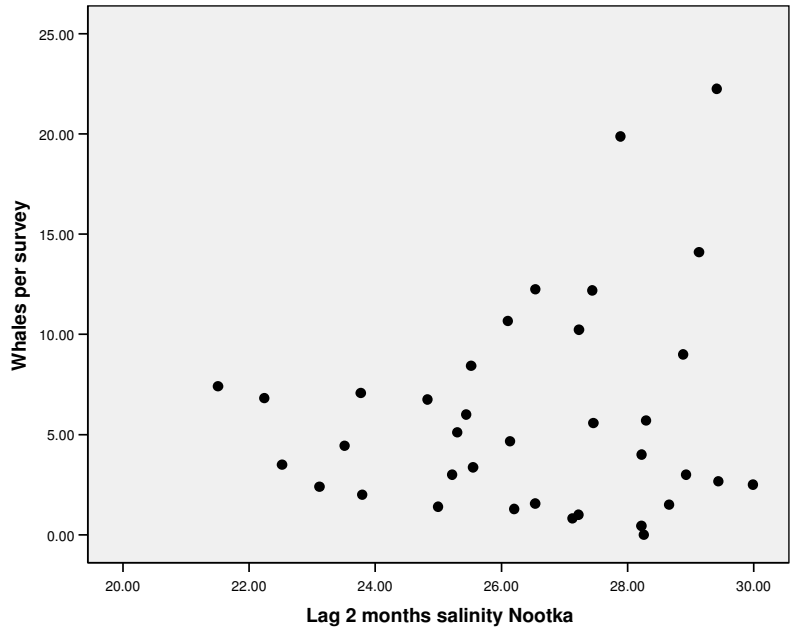
Lag 2 months salinity Amphitrite vs. whales per survey	Lag 3 months salinity Amphitrite vs. whales per survey
	

Lag 12 months salinity Amphitrite vs. whales per survey	Salinity Nootka vs. whales per survey
	

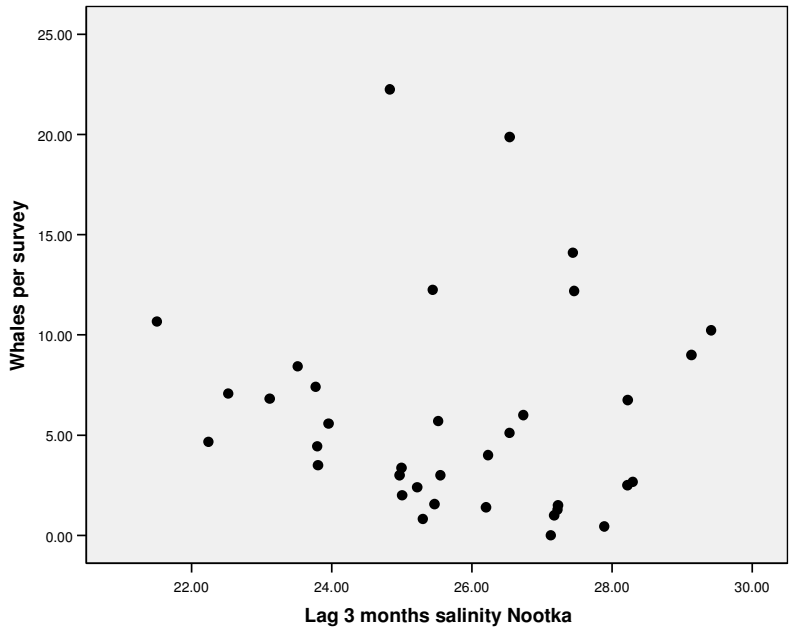
Lag 1 month salinity Nootka vs. whales per survey



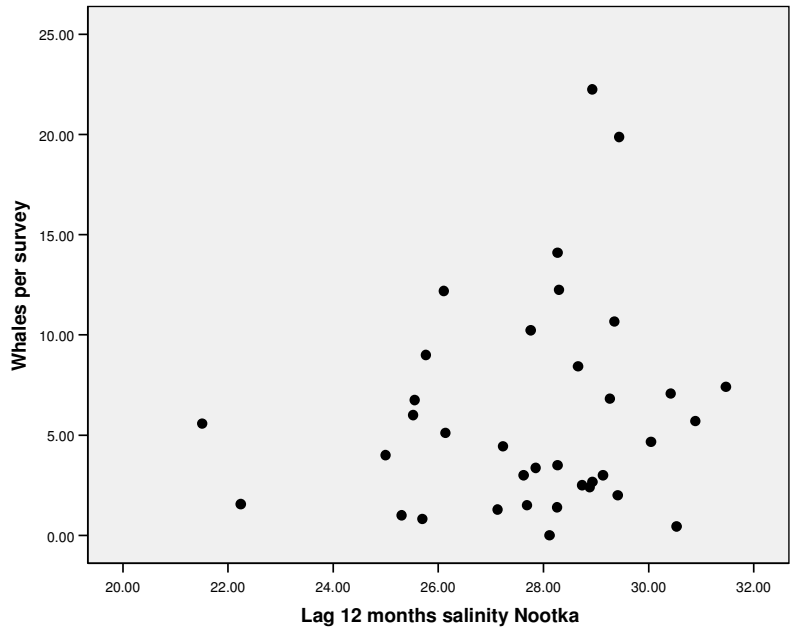
Lag 2 months salinity Nootka vs. whales per survey

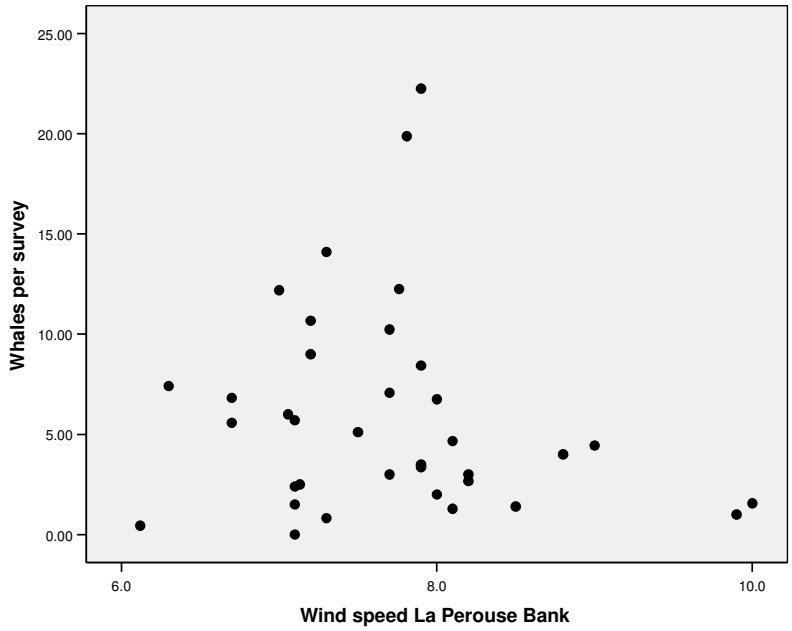
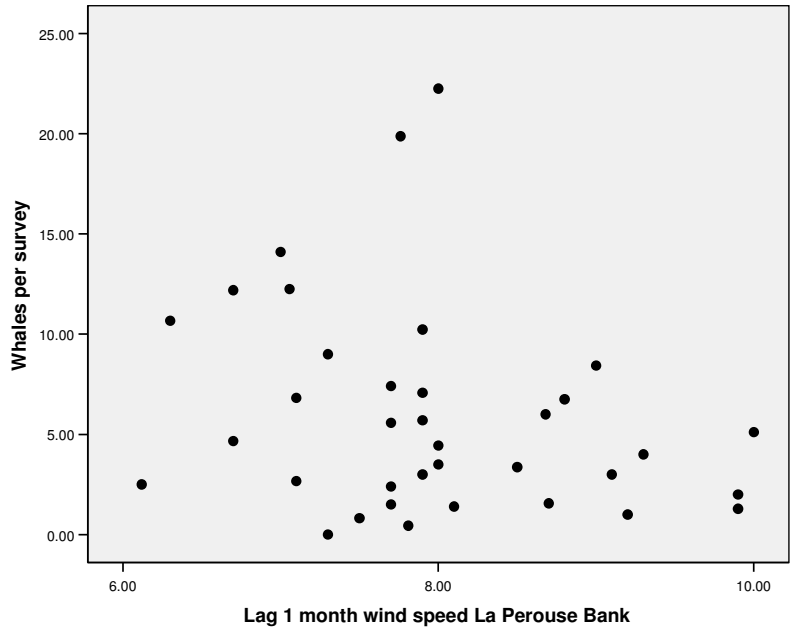


Lag 3 months salinity Nootka vs. whales per survey

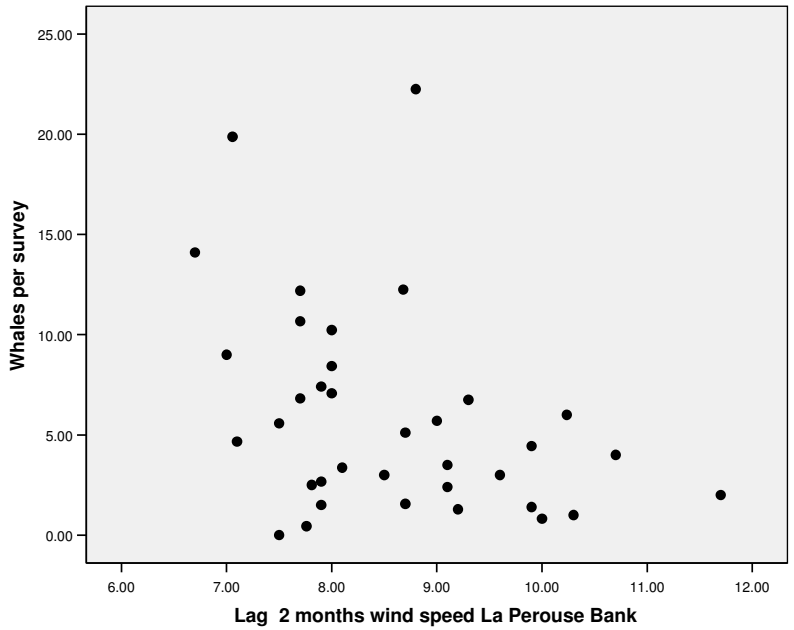


Lag 12 months salinity Nootka vs. whales per survey

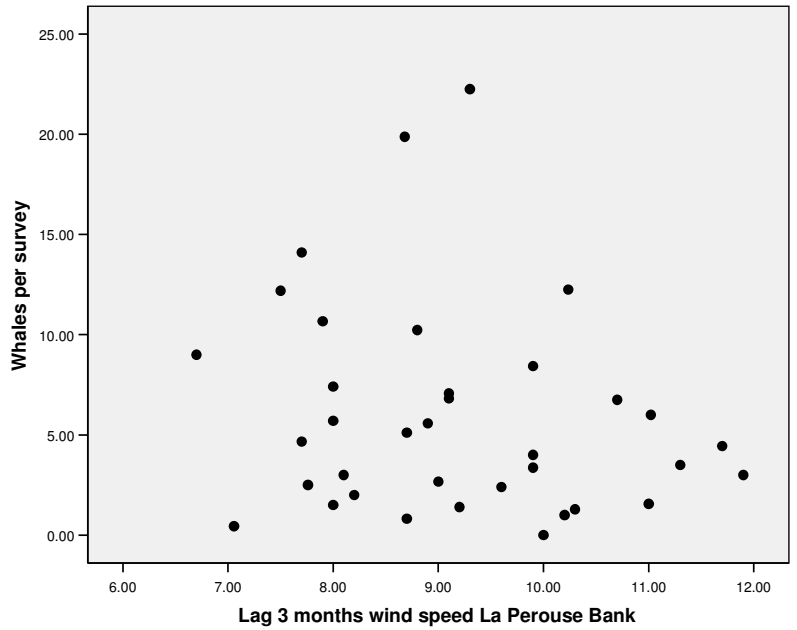


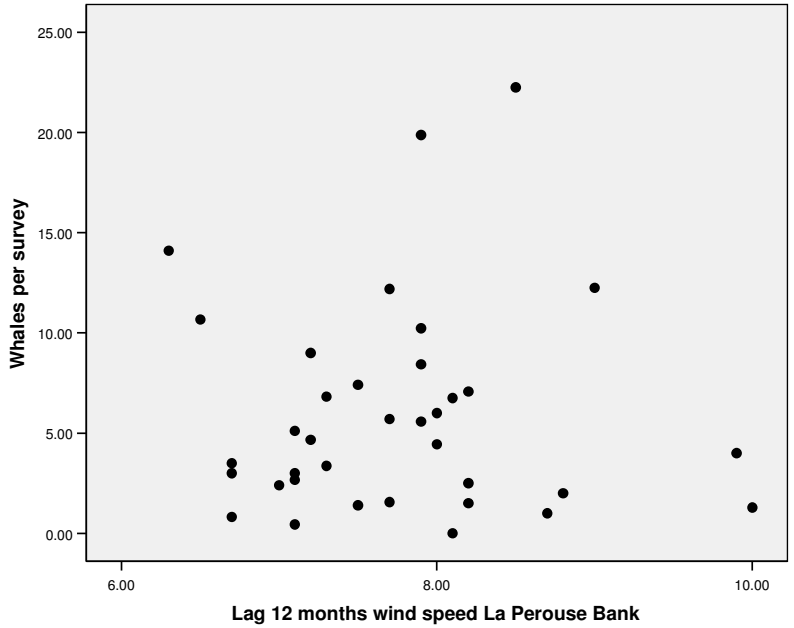
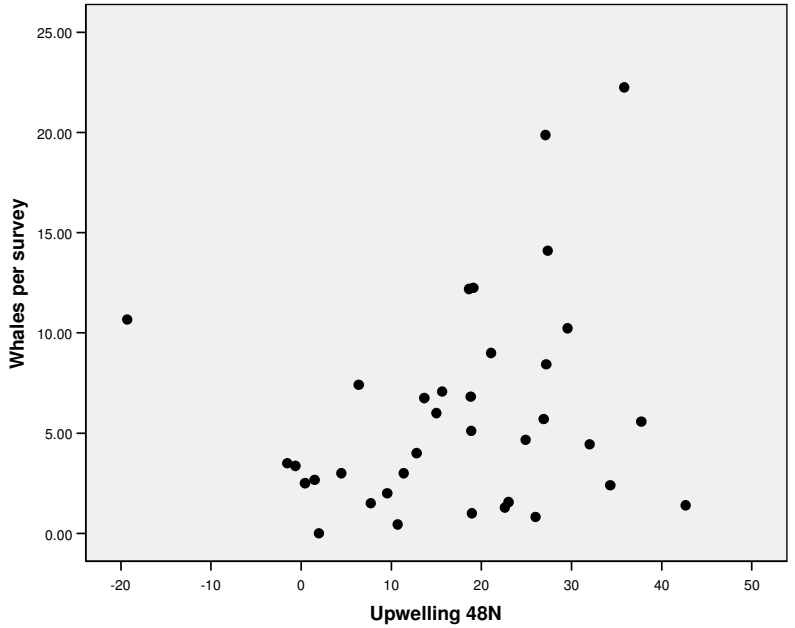
Wind speed La Perouse Bank vs. whales per survey	Lag 1 month wind speed La Perouse Bank vs. whales per survey
	

Lag 2 months wind speed La Perouse Bank vs. whales per survey

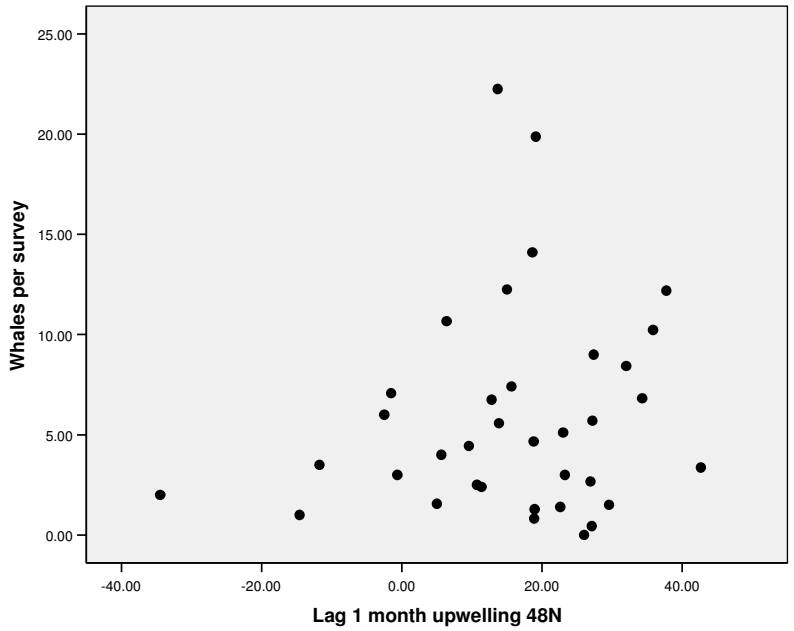


Lag 3 months wind speed La Perouse Bank vs. whales per survey

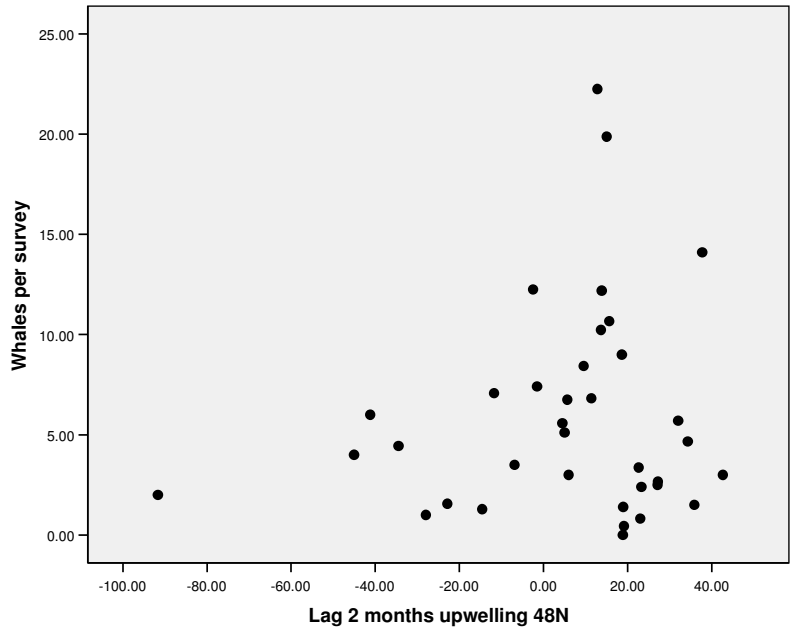


Lag 12 months wind speed La Perouse Bank vs. whales per survey	Upwelling 48N vs. whales per survey
	

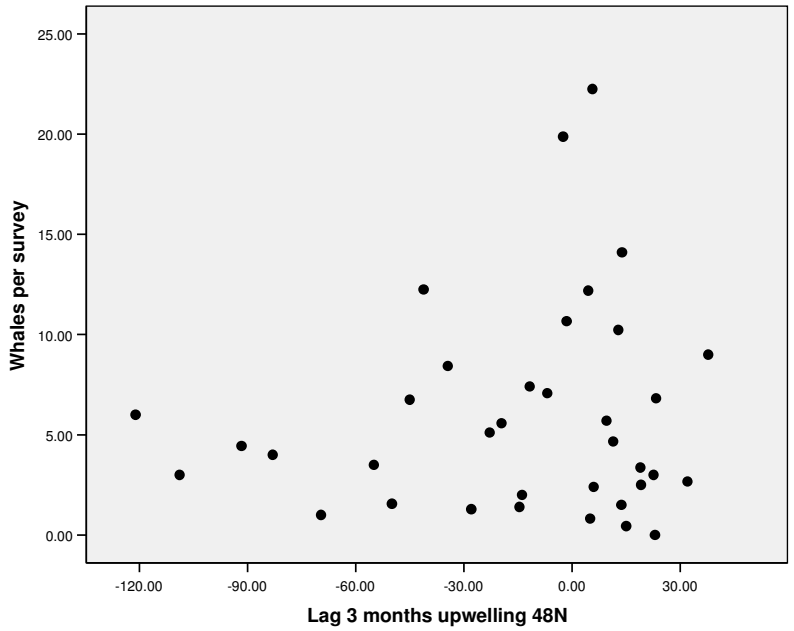
Lag 1 month upwelling 48N vs. whales per survey



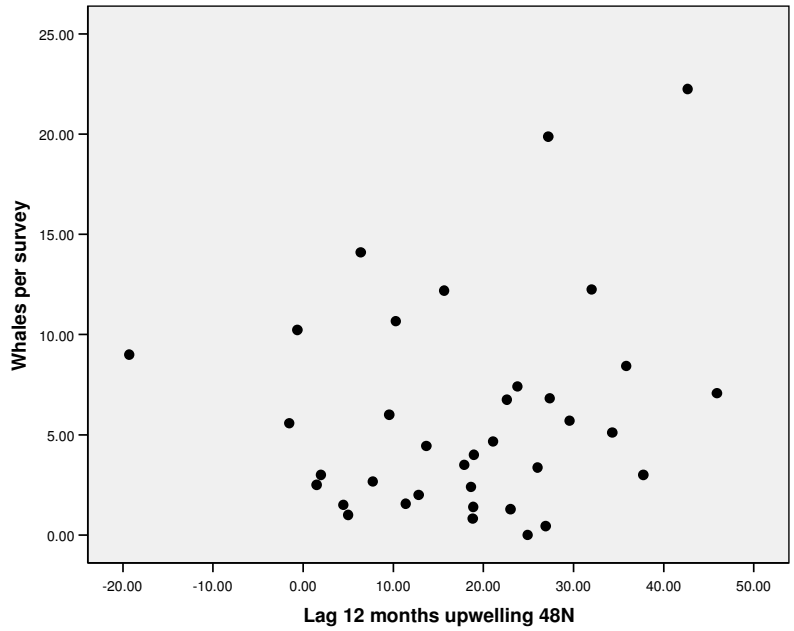
Lag 2 months upwelling 48N vs. whales per survey



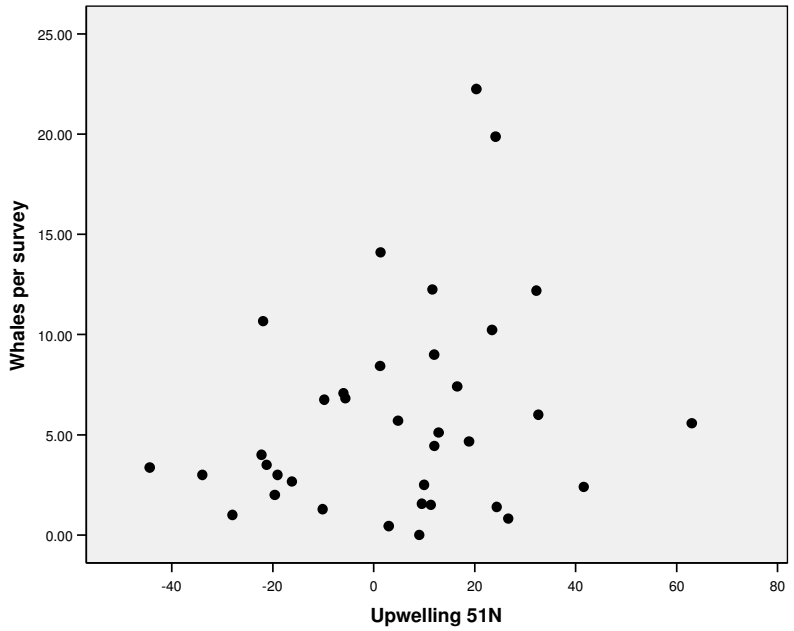
Lag 3 months upwelling 48N vs. whales per survey



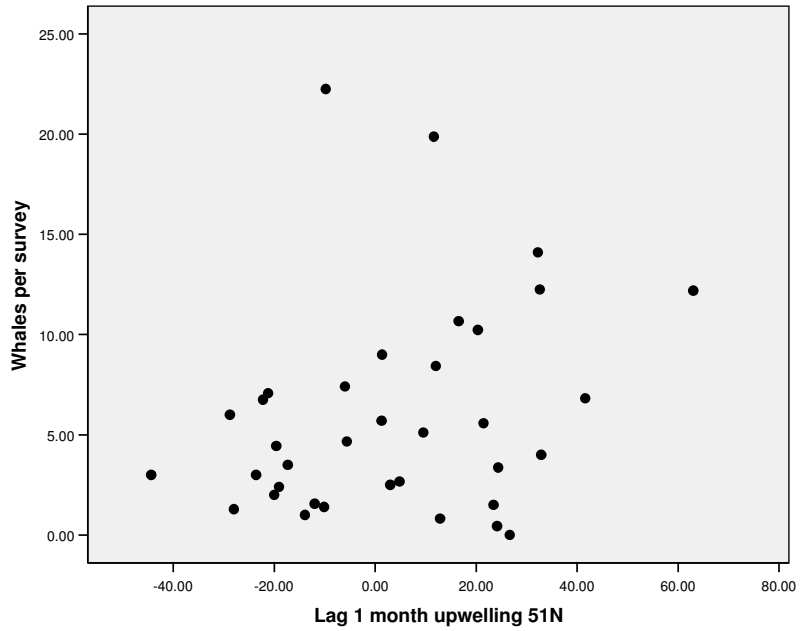
Lag 12 months upwelling 48N vs. whales per survey



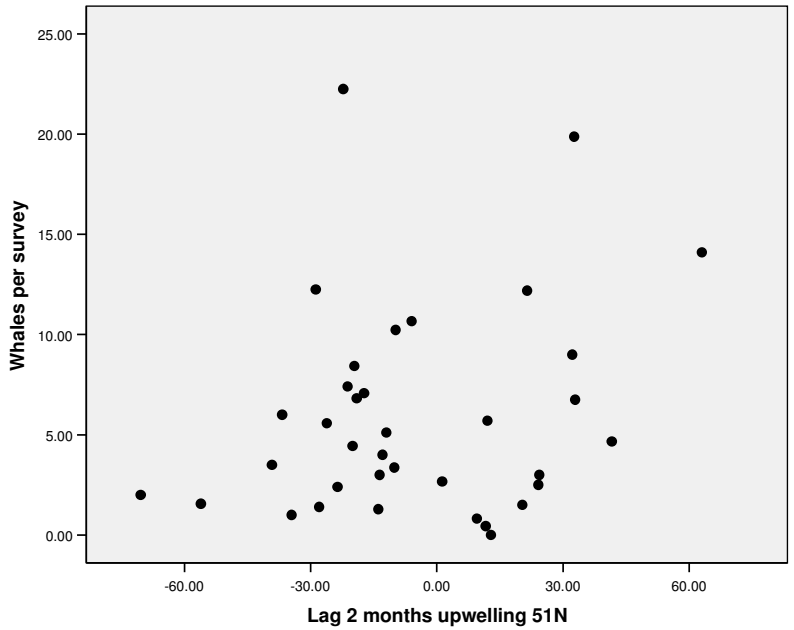
Upwelling 51N vs. whales per survey



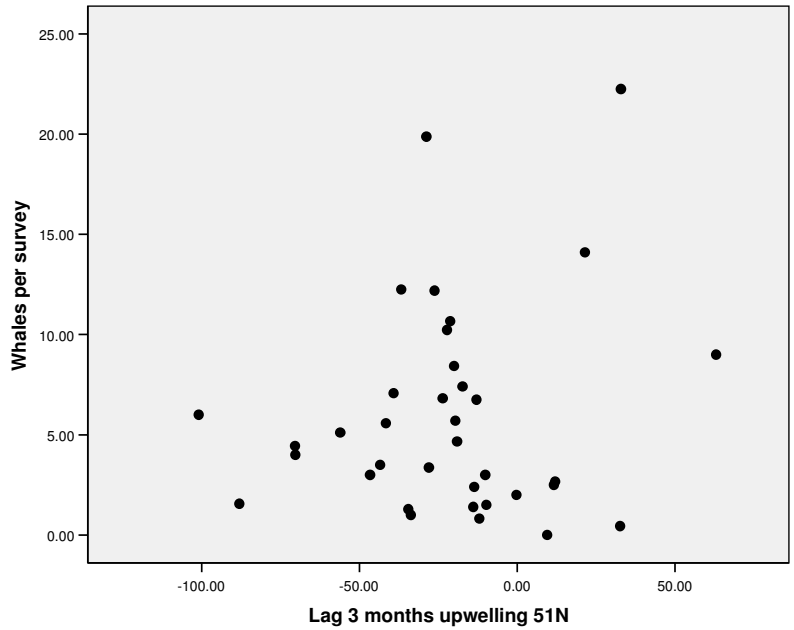
Lag 1 month upwelling 51N vs. whales per survey



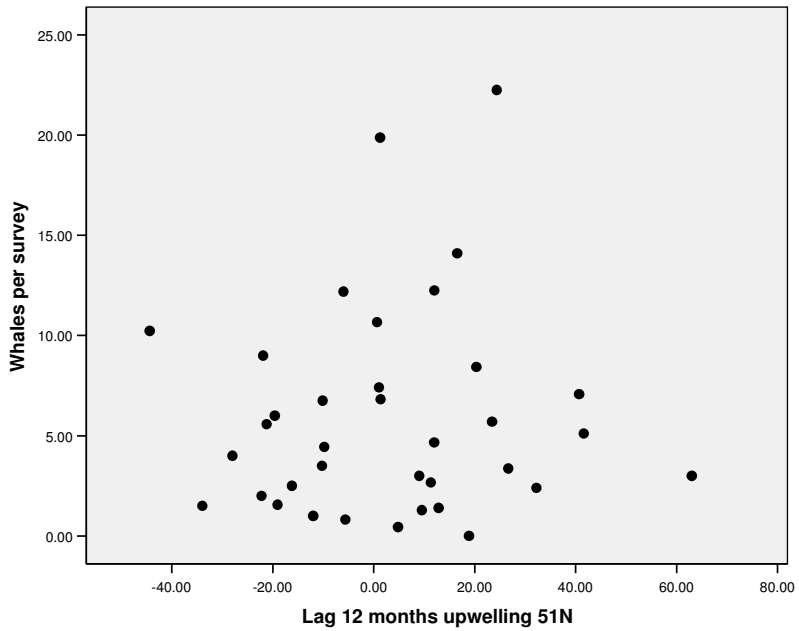
Lag 2 months upwelling 51N vs. whales per survey



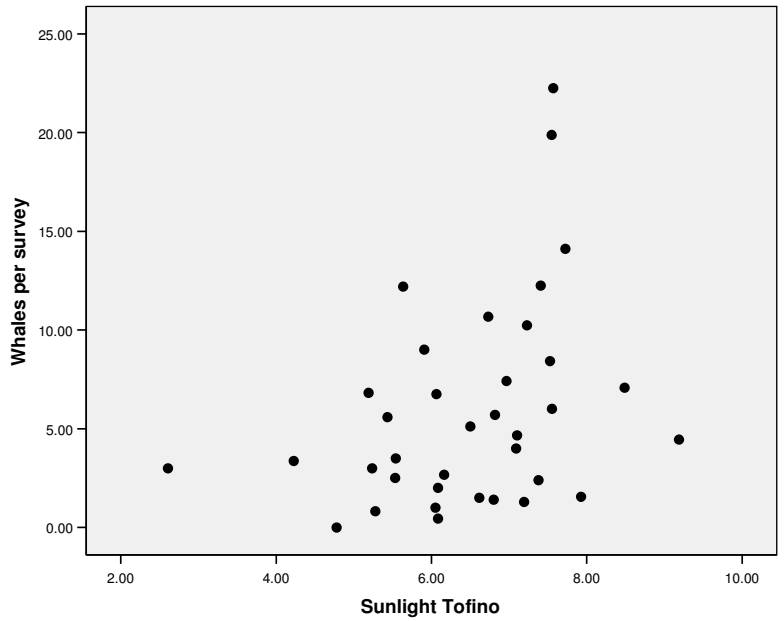
Lag 3 months upwelling 51N vs. whales per survey



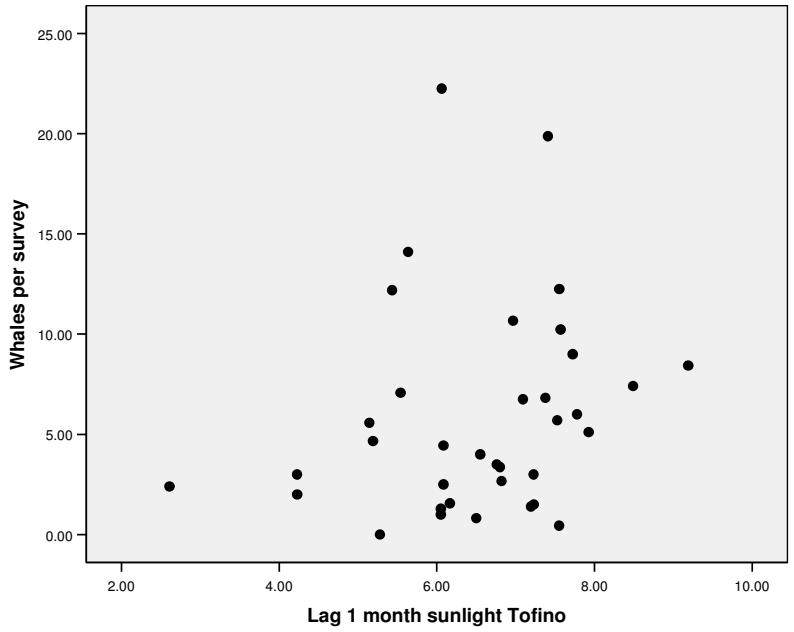
Lag 12 months upwelling 51N vs. whales per survey



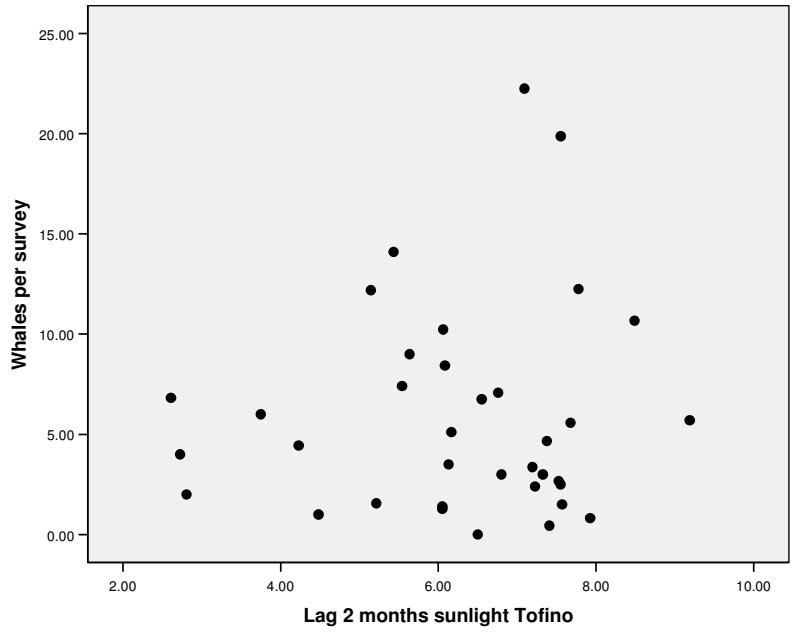
Sunlight Tofino vs. whales per survey



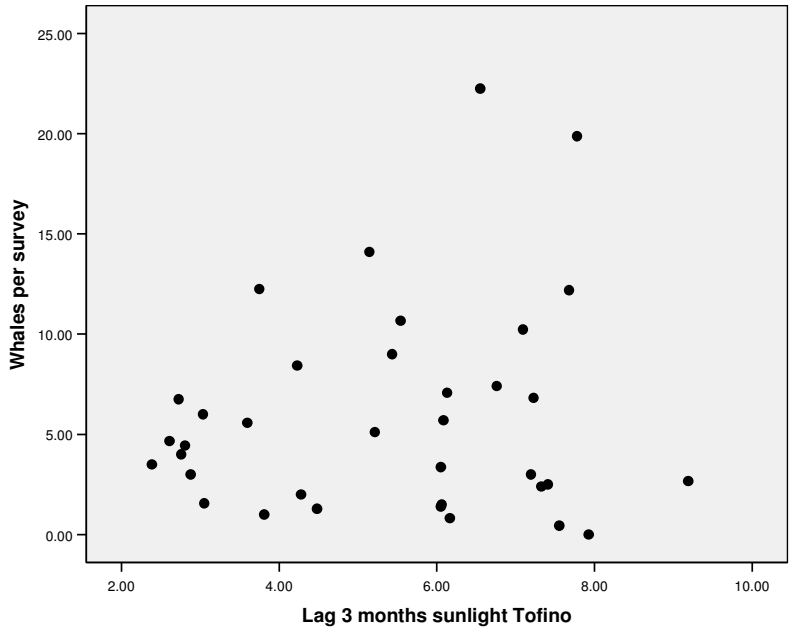
Lag 1 month sunlight Tofino vs. whales per survey



Lag 2 months sunlight Tofino vs. whales per survey



Lag 3 months sunlight Tofino vs. whales per survey



Lag 12 months sunlight Tofino vs. whales per survey

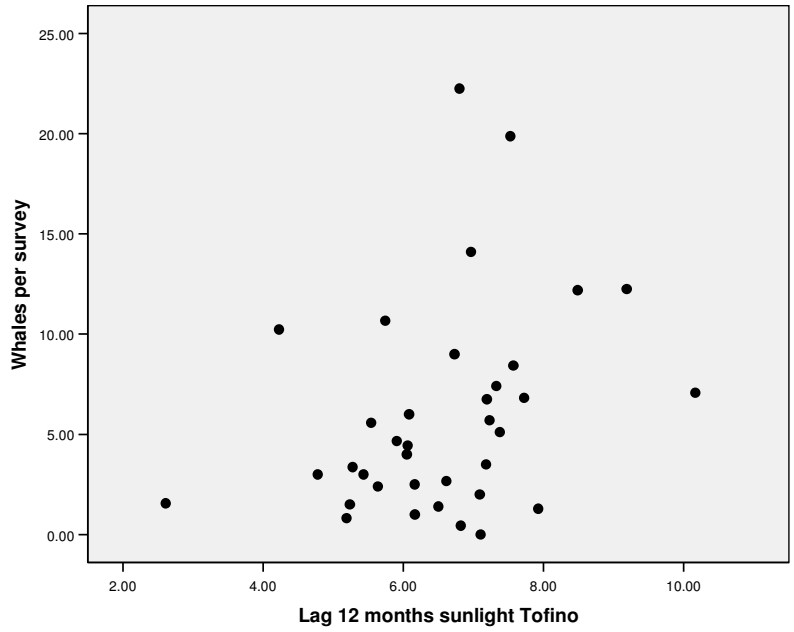
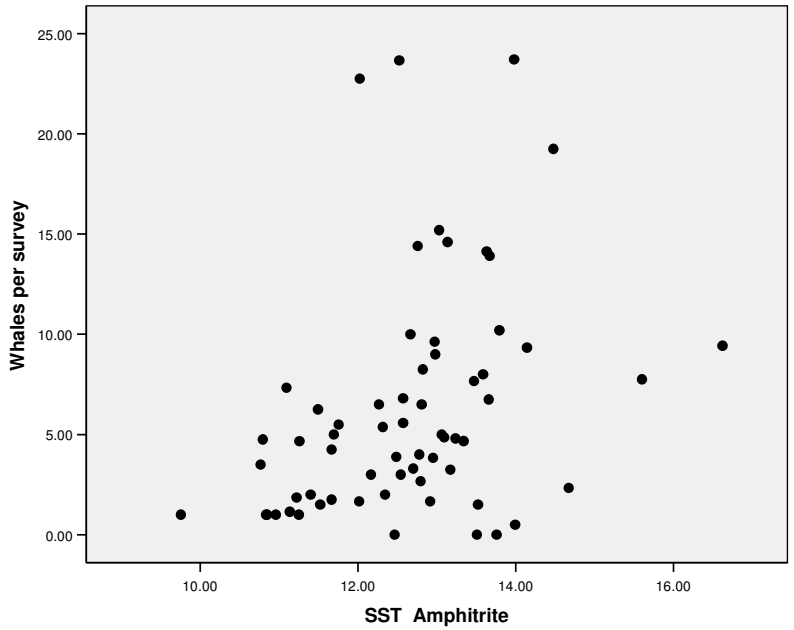
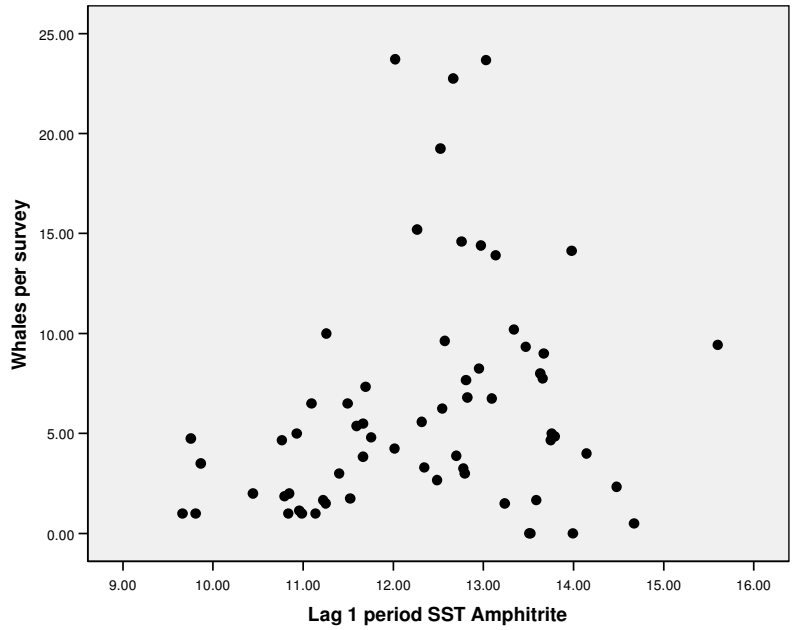


Figure 6. Scatterplots – semi-monthly scale.

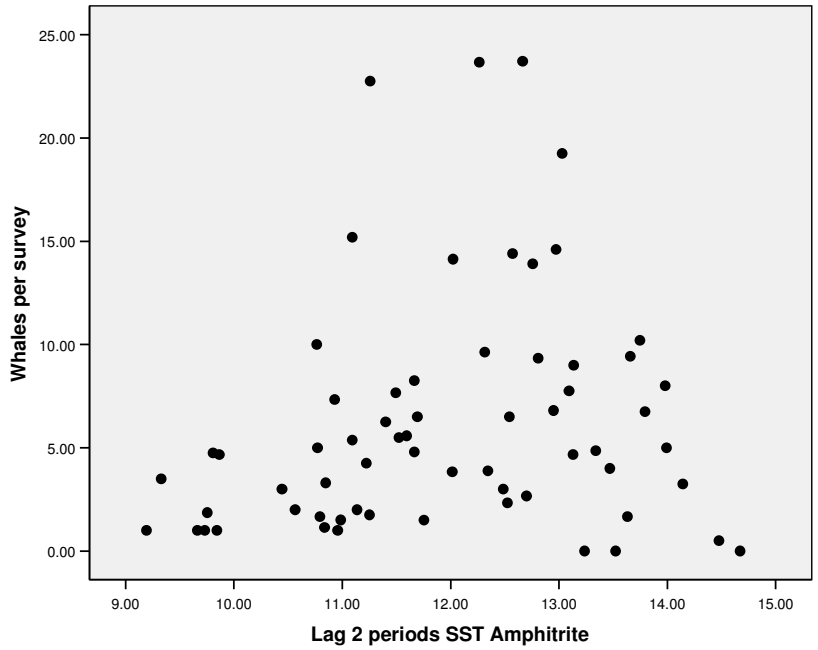
SST Amphitrite vs. whales per survey



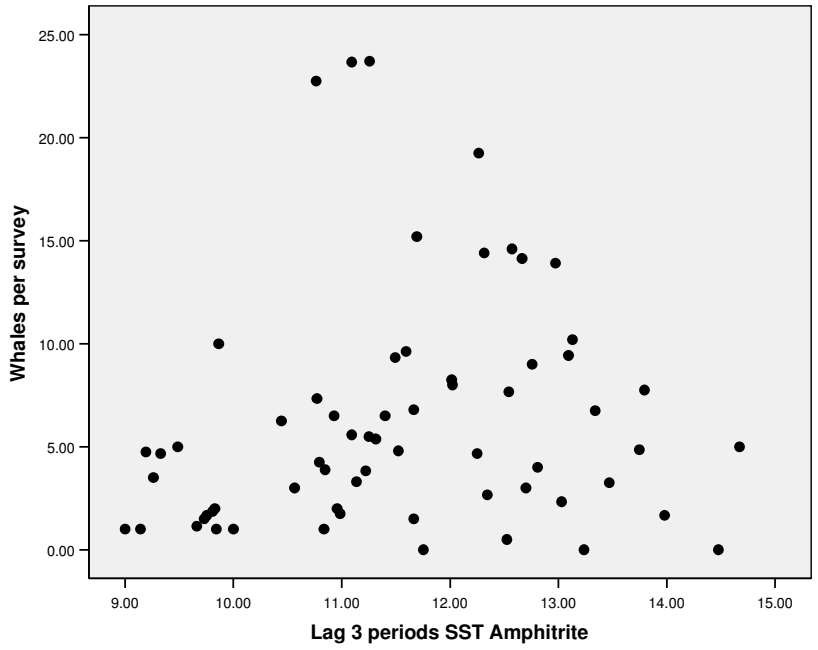
Lag 1 period SST Amphitrite vs. whales per survey



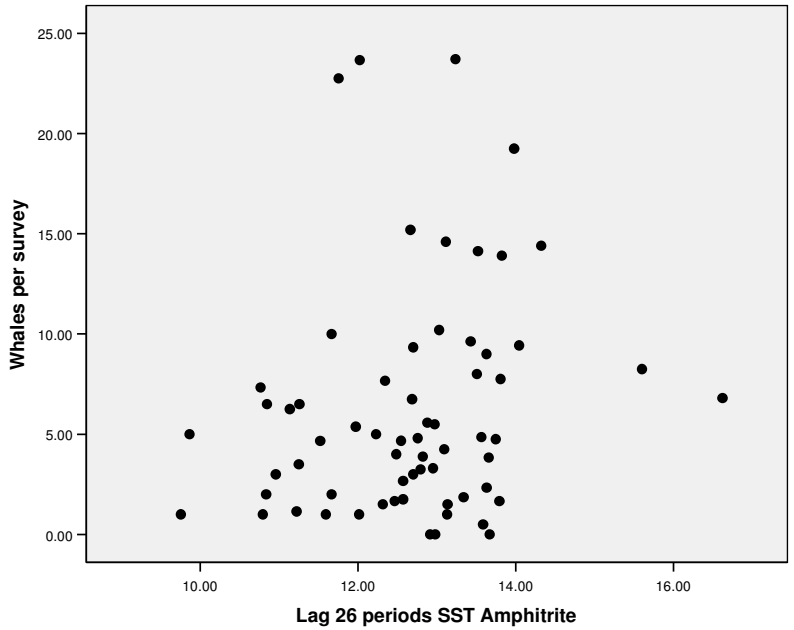
Lag 2 periods SST Amphitrite vs. whales per survey



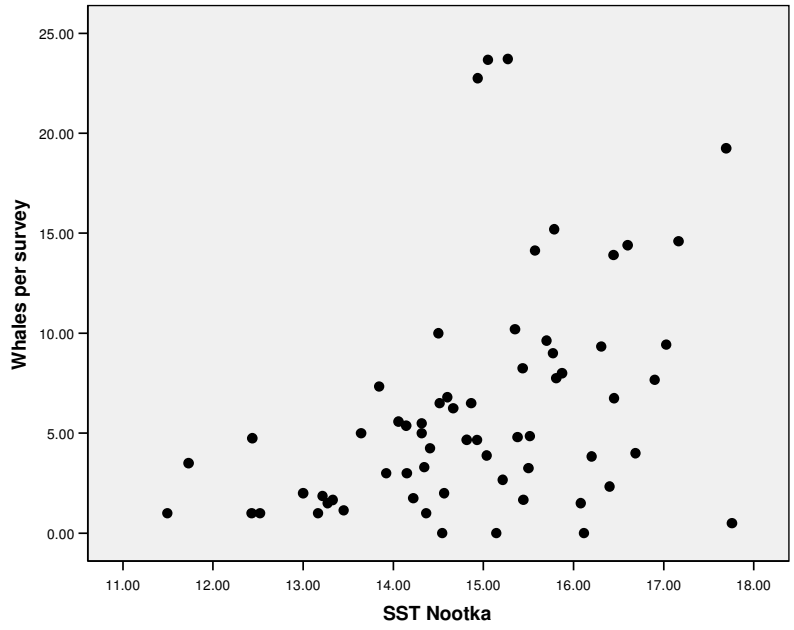
Lag 3 periods SST Amphitrite vs. whales per survey



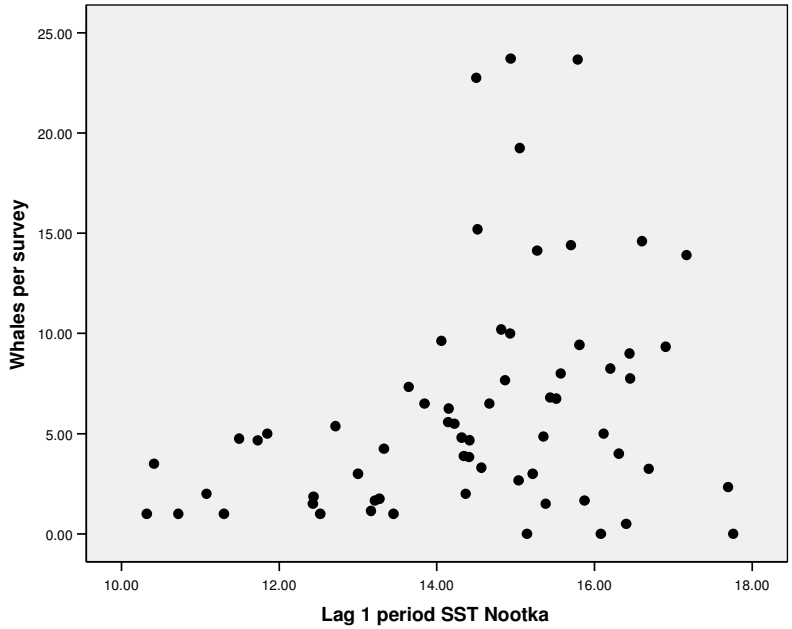
Lag 26 periods SST Amphitrite vs. whales per survey



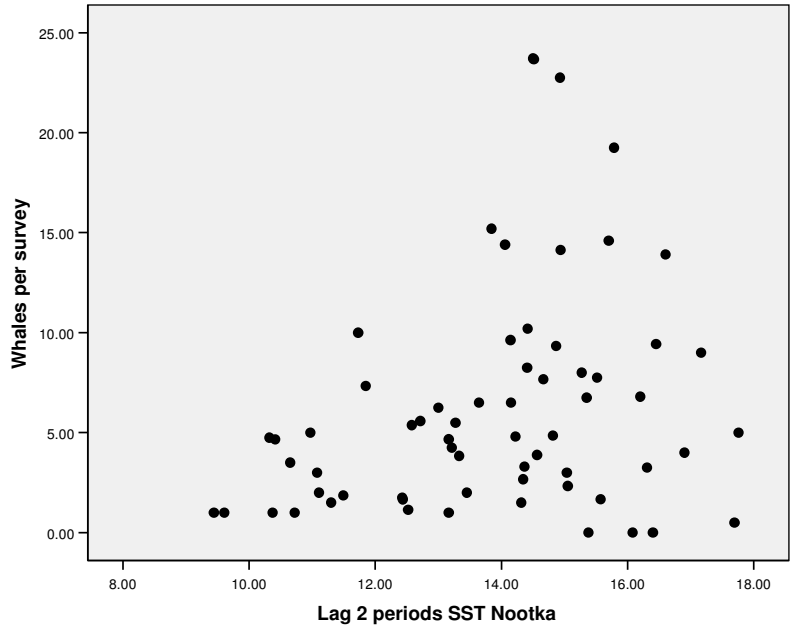
SST Nootka vs. whales per survey



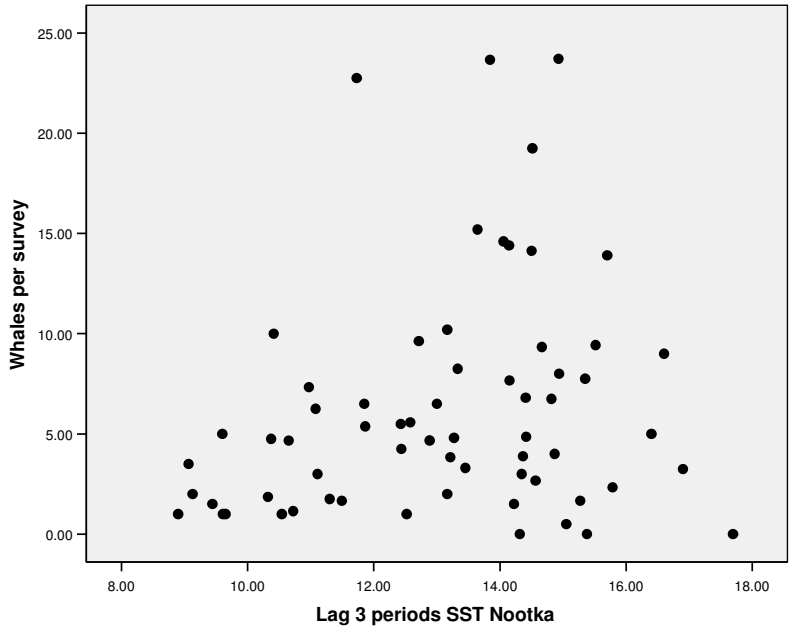
Lag 1 period SST Nootka vs. whales per survey



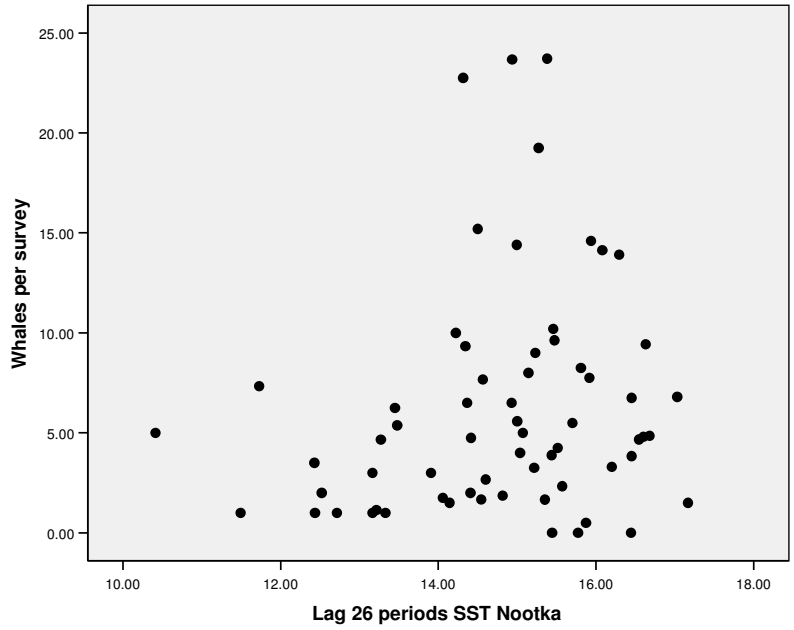
Lag 2 periods SST Nootka vs. whales per survey



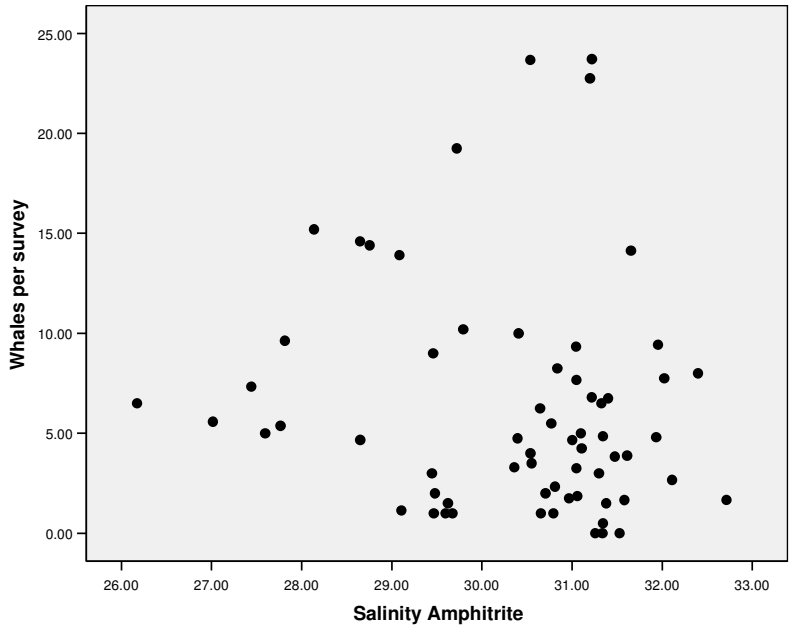
Lag 3 periods SST Nootka vs. whales per survey



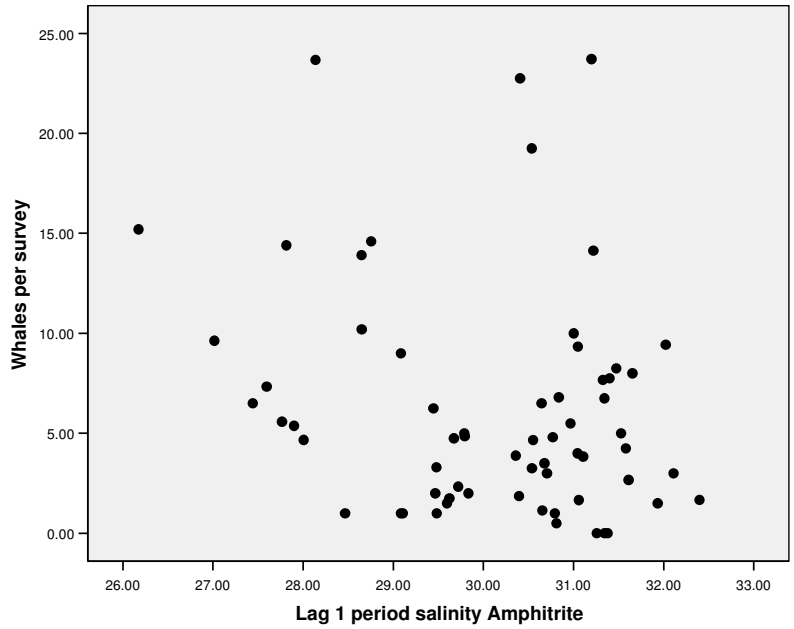
Lag 26 periods SST Nootka vs. whales per survey



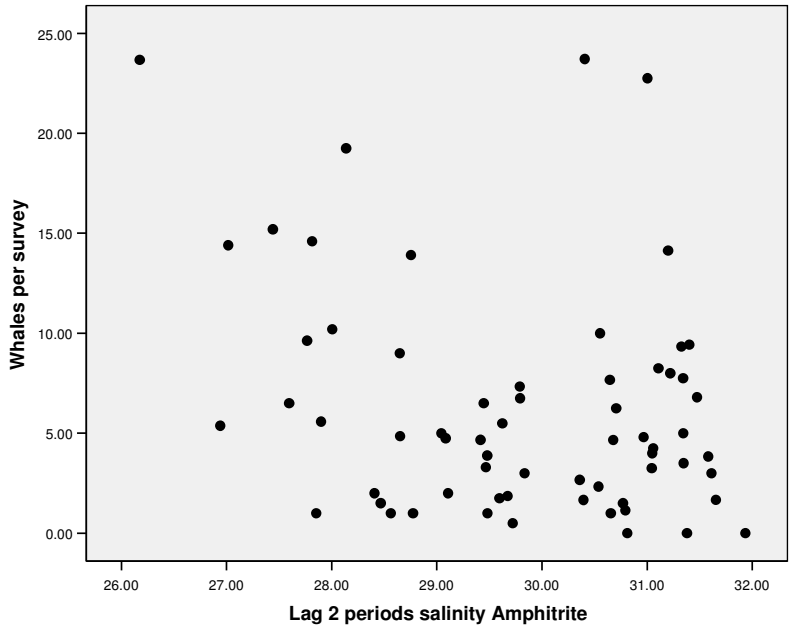
Salinity Amphitrite vs. whales per survey



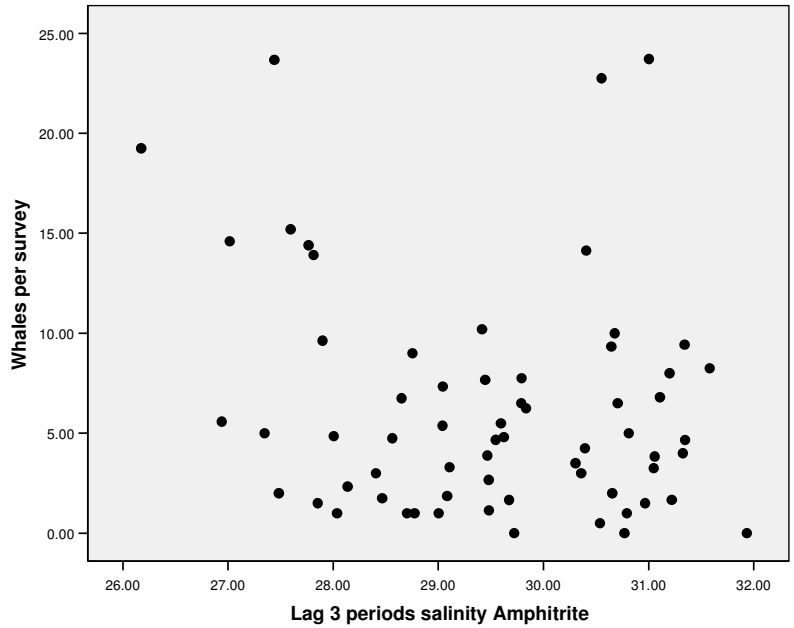
Lag 1 period salinity Amphitrite vs. whales per survey

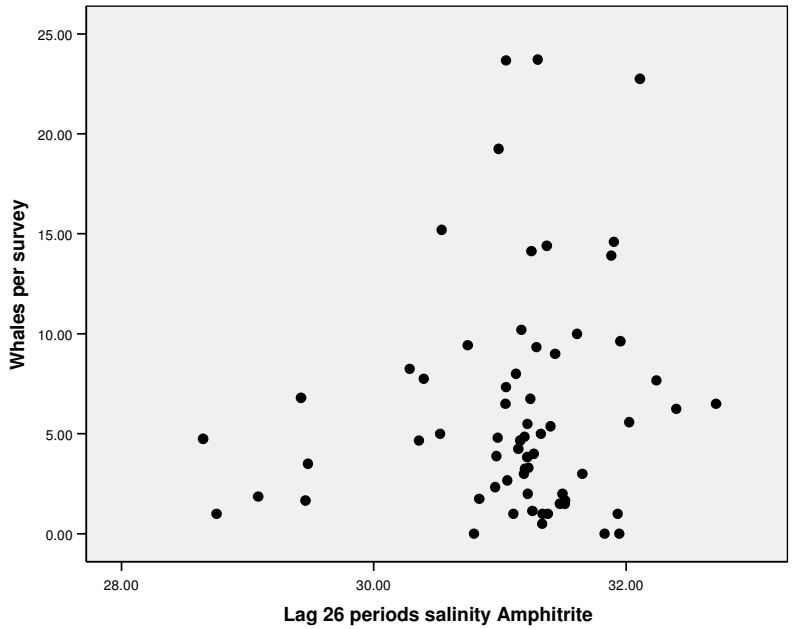
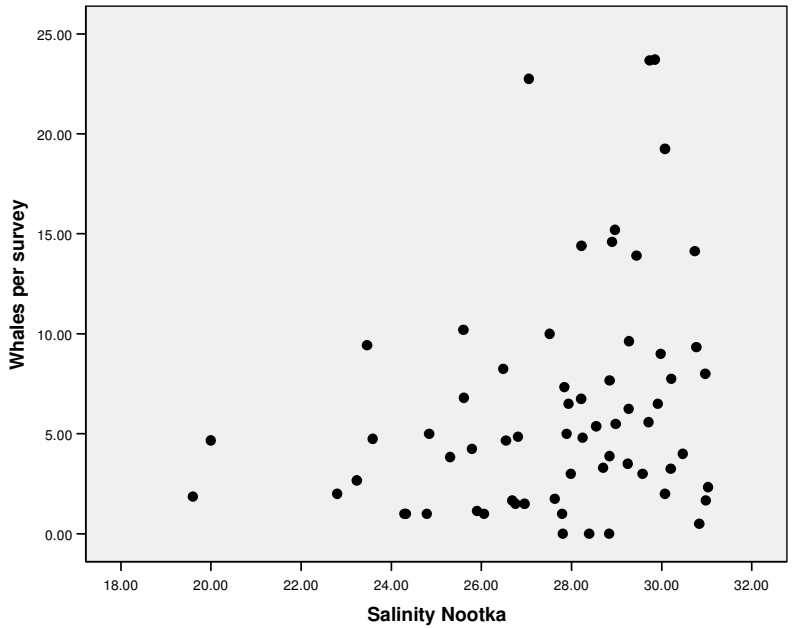


Lag 2 periods salinity Amphitrite vs. whales per survey

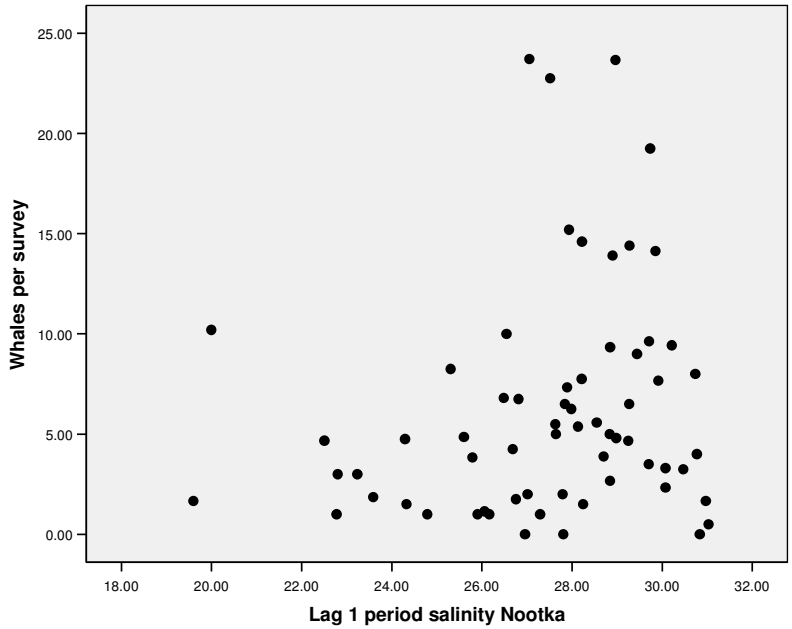


Lag 3 periods salinity Amphitrite vs. whales per survey

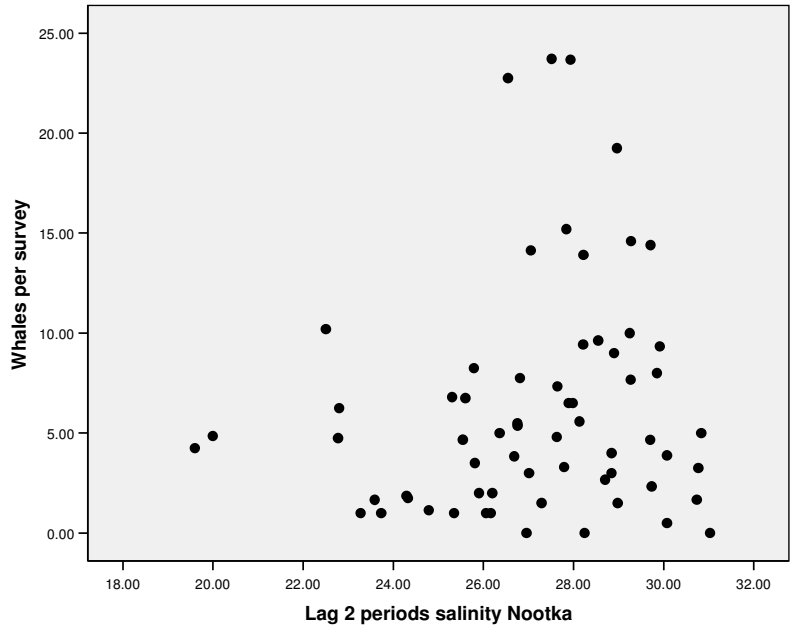


Lag 26 periods salinity Amphitrite vs. whales per survey	Salinity Nootka vs. whales per survey
	

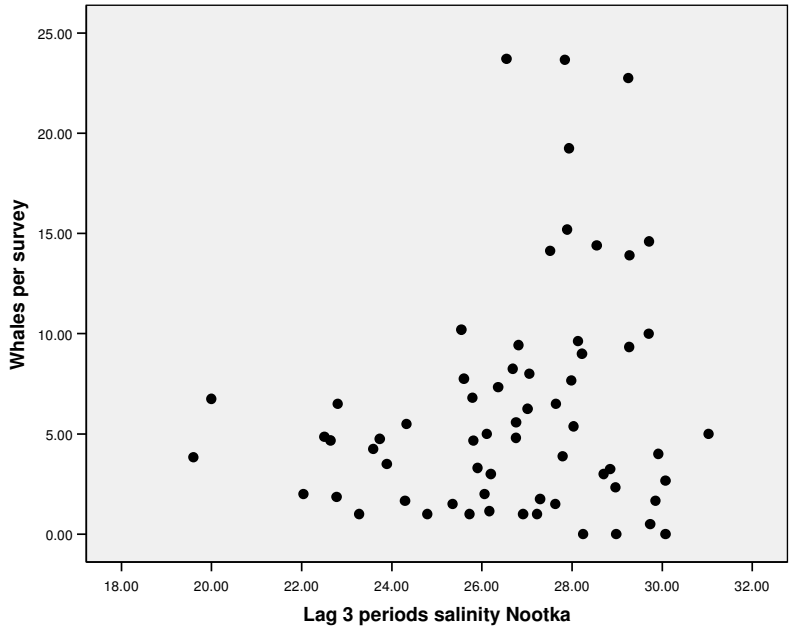
Lag 1 period salinity Nootka vs. whales per survey



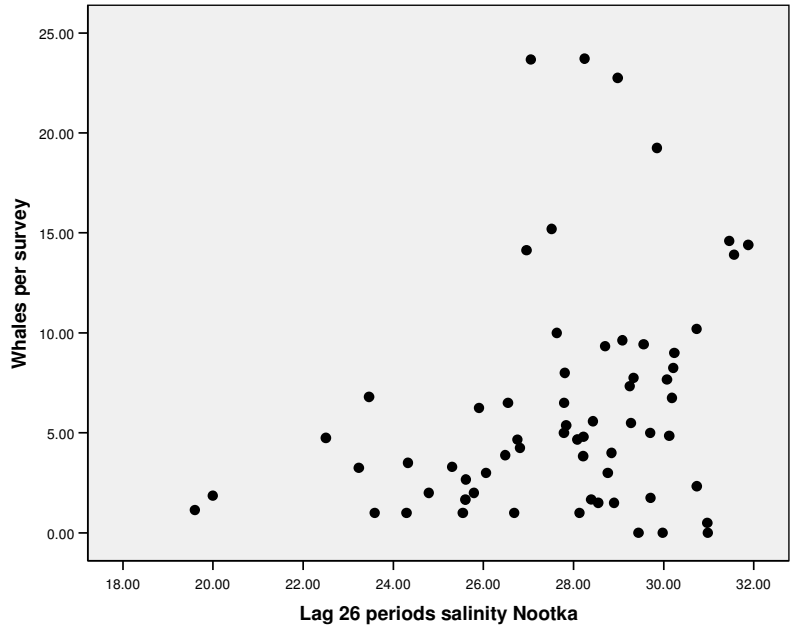
Lag 2 periods salinity Nootka vs. whales per survey

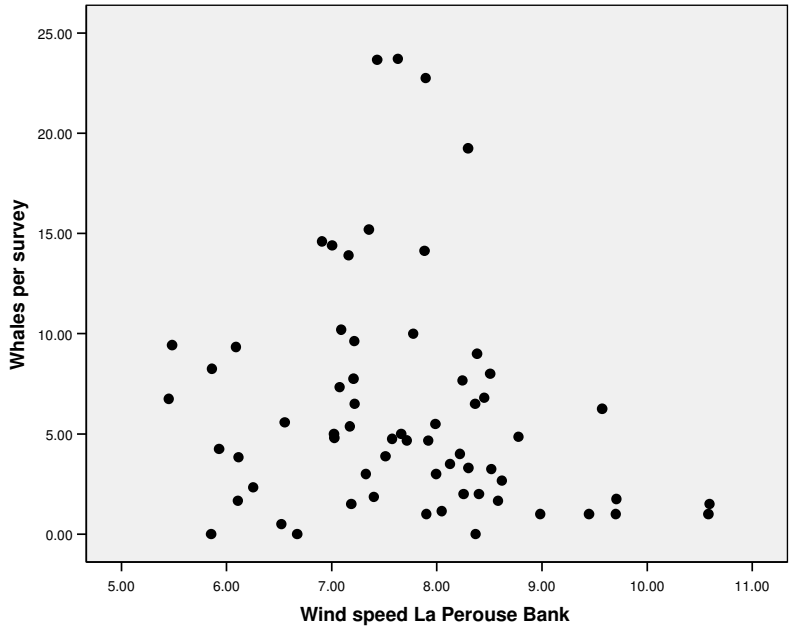
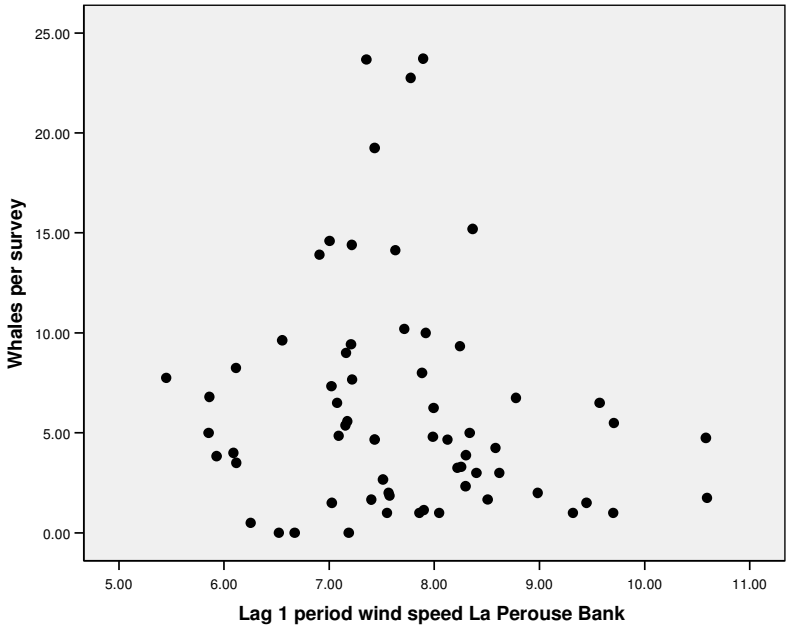


Lag 3 periods salinity Nootka vs. whales per survey

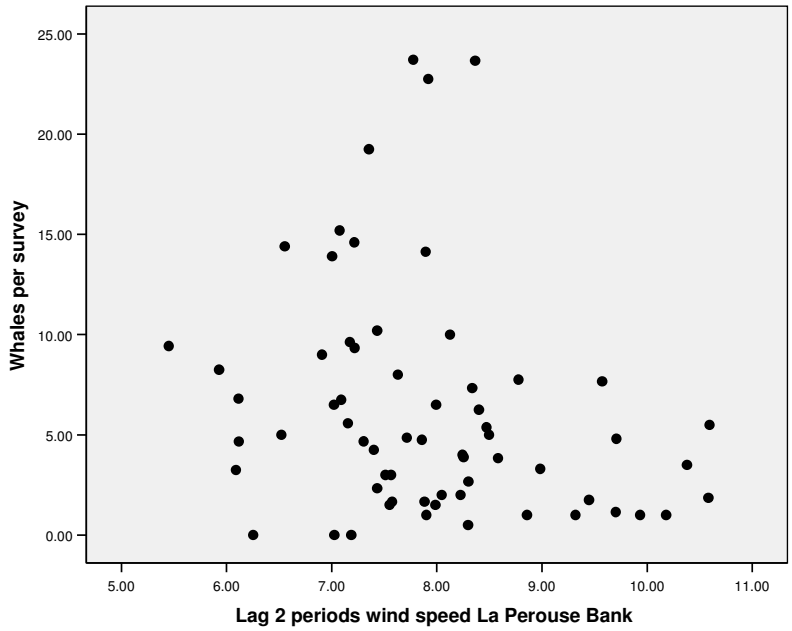


Lag 26 periods salinity Nootka vs. whales per survey

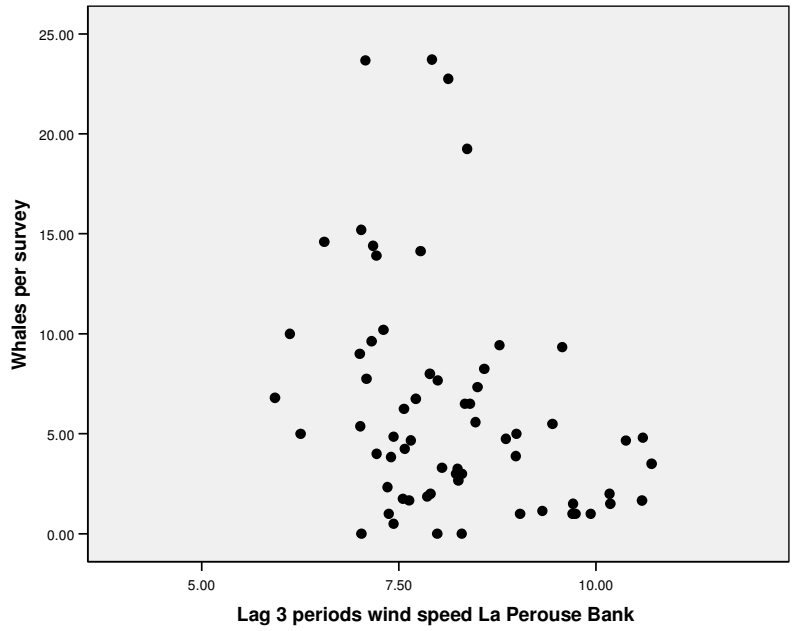


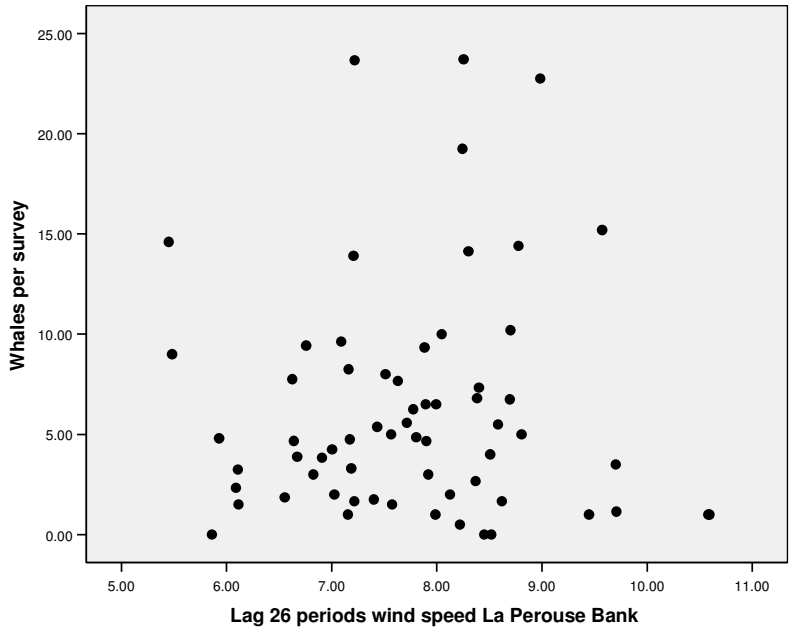
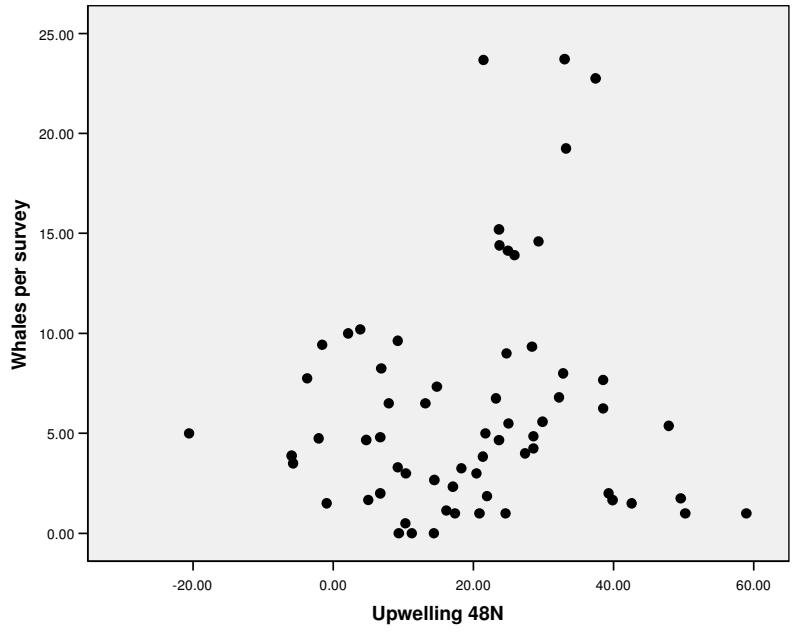
Wind speed La Perouse Bank vs. whales per survey	Lag 1 period wind speed La Perouse Bank vs. whales per survey
	

Lag 2 periods wind speed La Perouse Bank vs. whales per survey

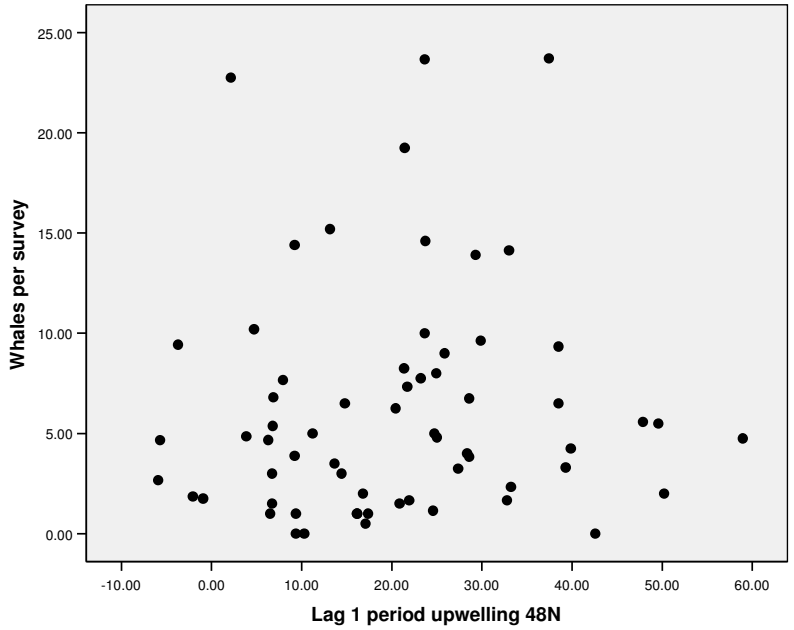


Lag 3 periods wind speed La Perouse Bank vs. whales per survey

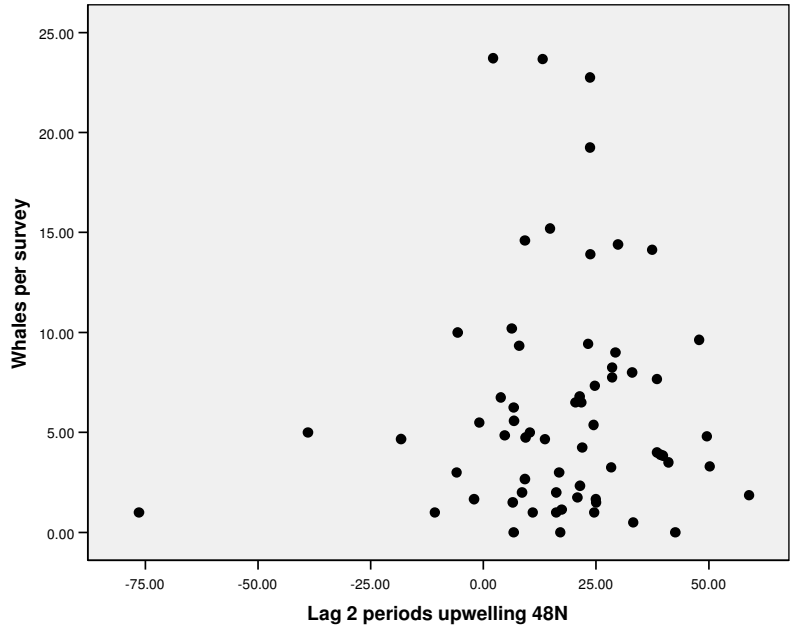


Lag 26 periods wind speed La Perouse Bank vs. whales per survey	Upwelling 48N vs. whales per survey
	

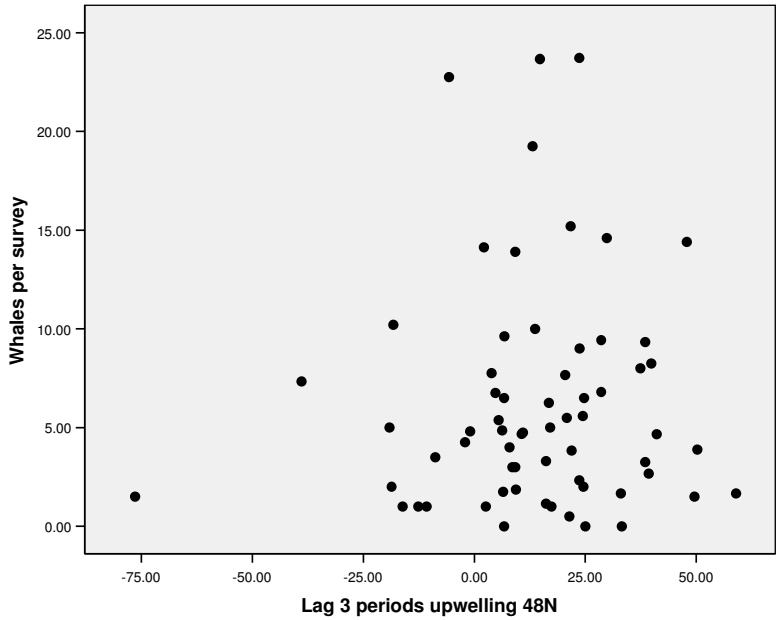
Lag 1 period upwelling 48N vs. whales per survey



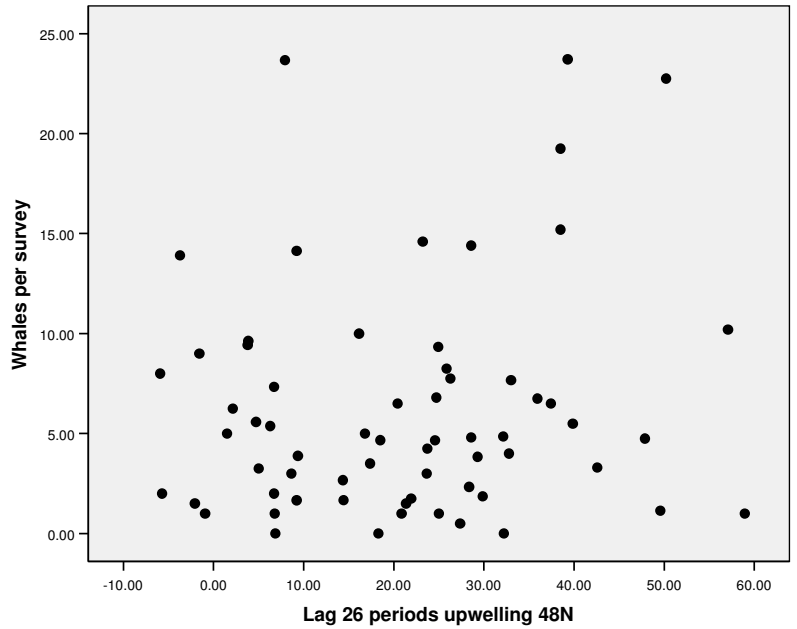
Lag 2 periods upwelling 48N vs. whales per survey



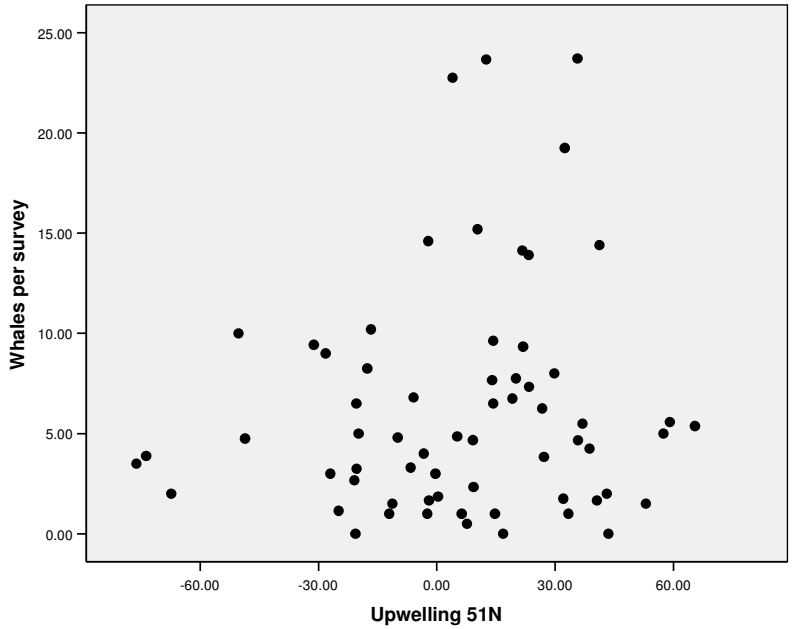
Lag 3 periods upwelling 48N vs. whales per survey



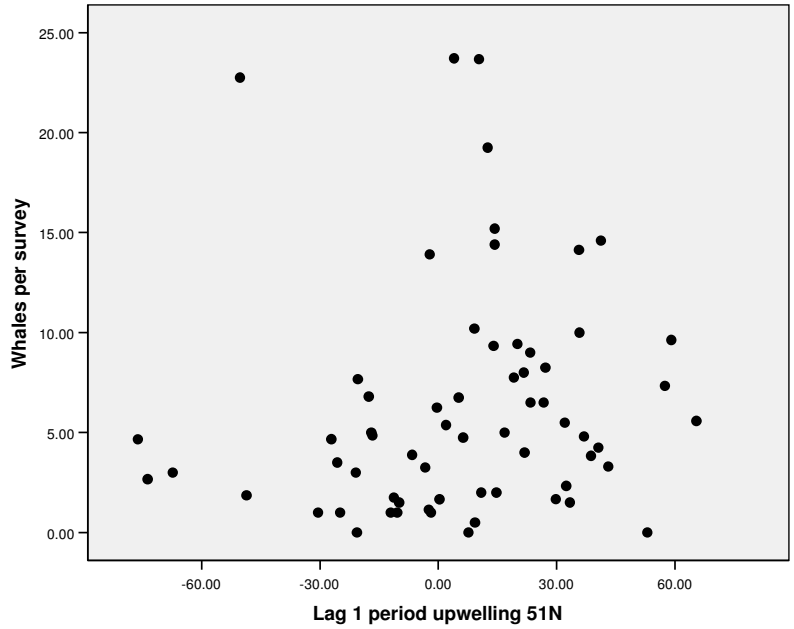
Lag 26 periods upwelling 48N vs. whales per survey



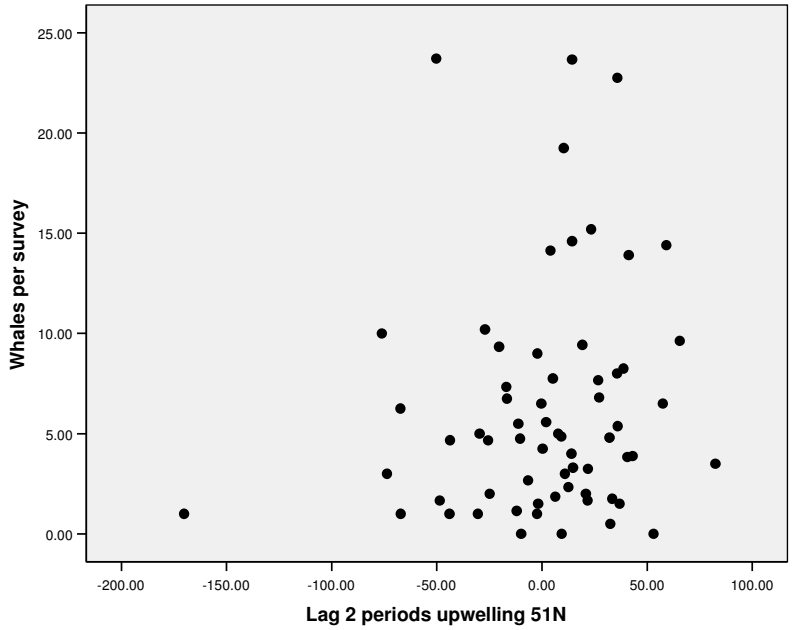
Upwelling 51N vs. whales per survey



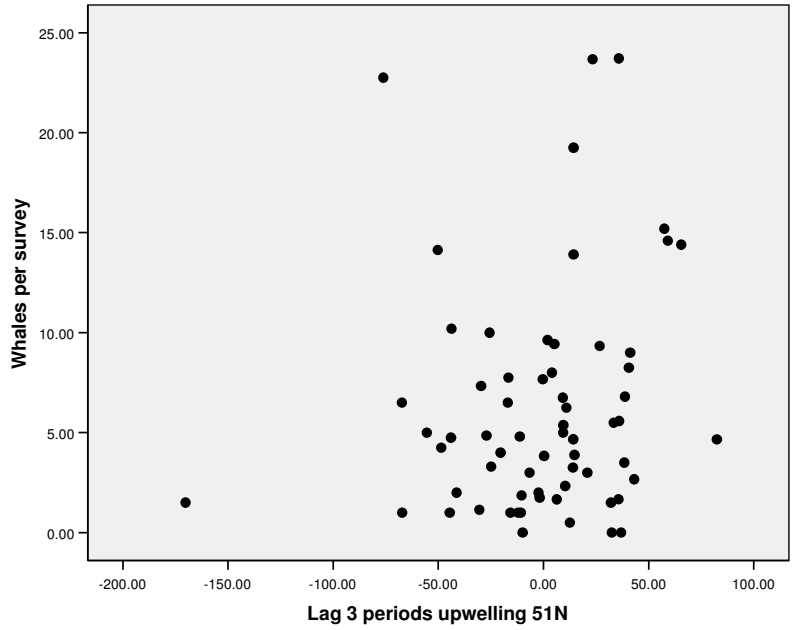
Lag 1 period upwelling 51N vs. whales per survey



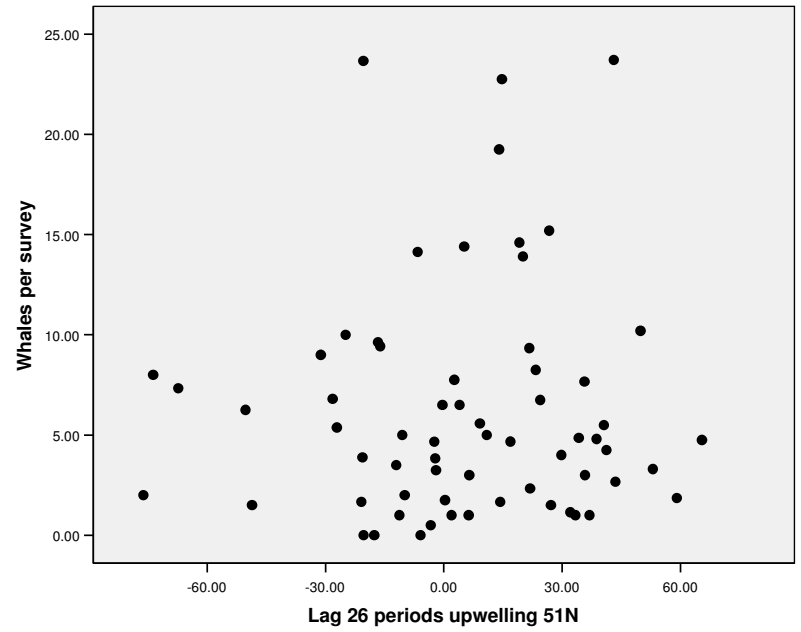
Lag 2 periods upwelling 51N vs. whales per survey



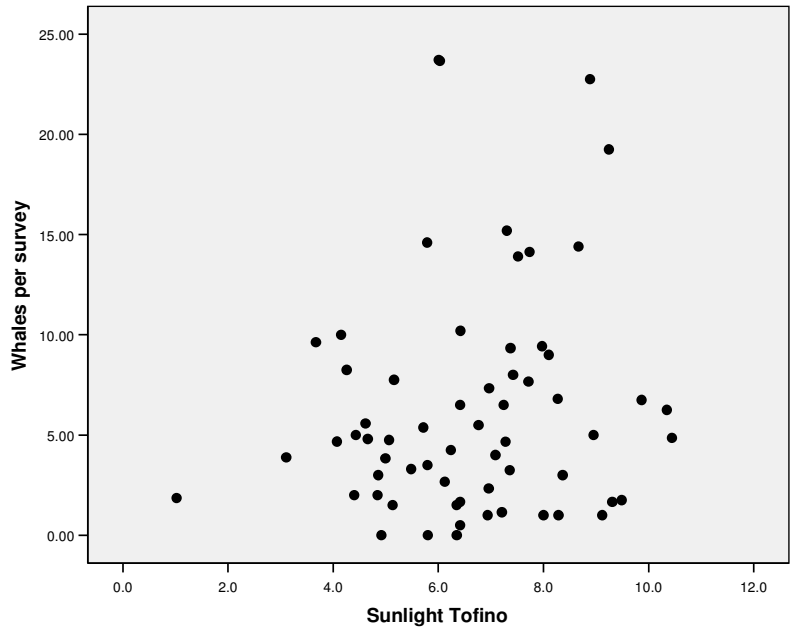
Lag 3 periods upwelling 51N vs. whales per survey



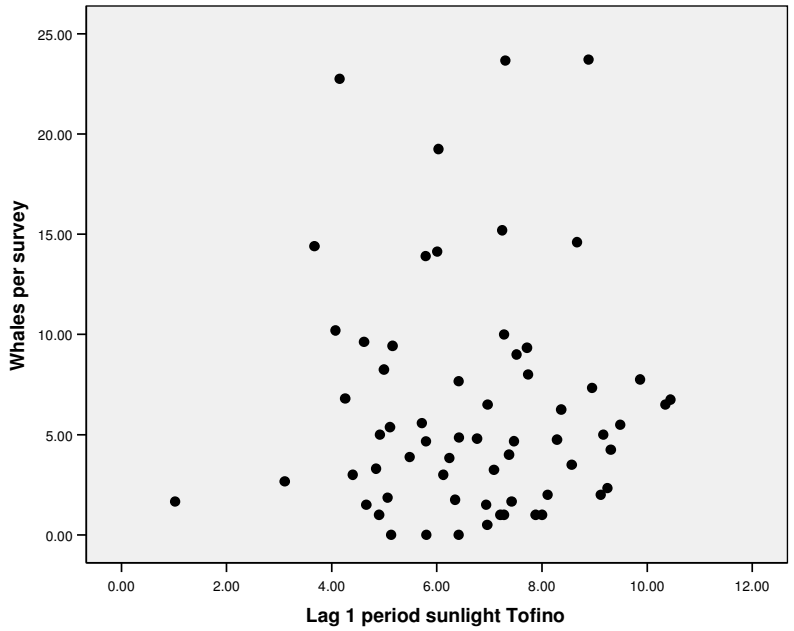
Lag 26 periods upwelling 51N vs. whales per survey



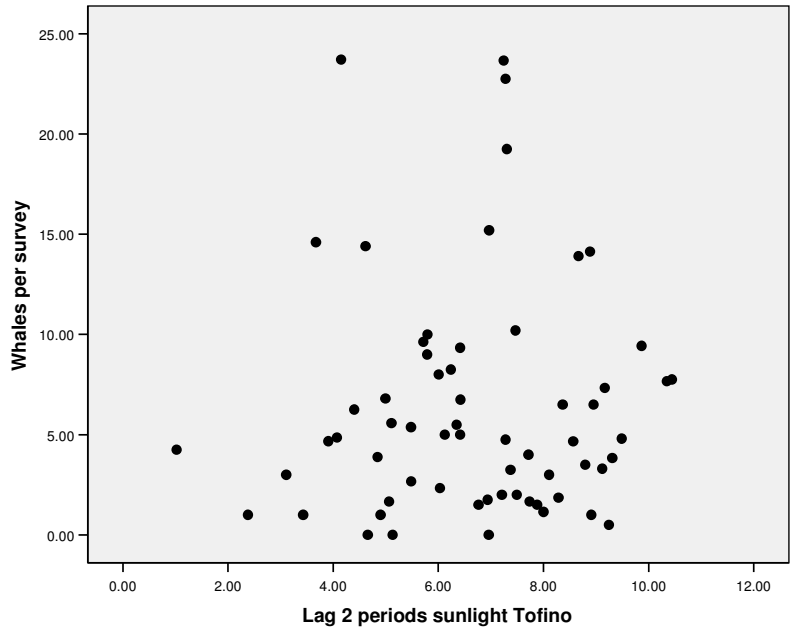
Sunlight Tofino vs. whales per survey



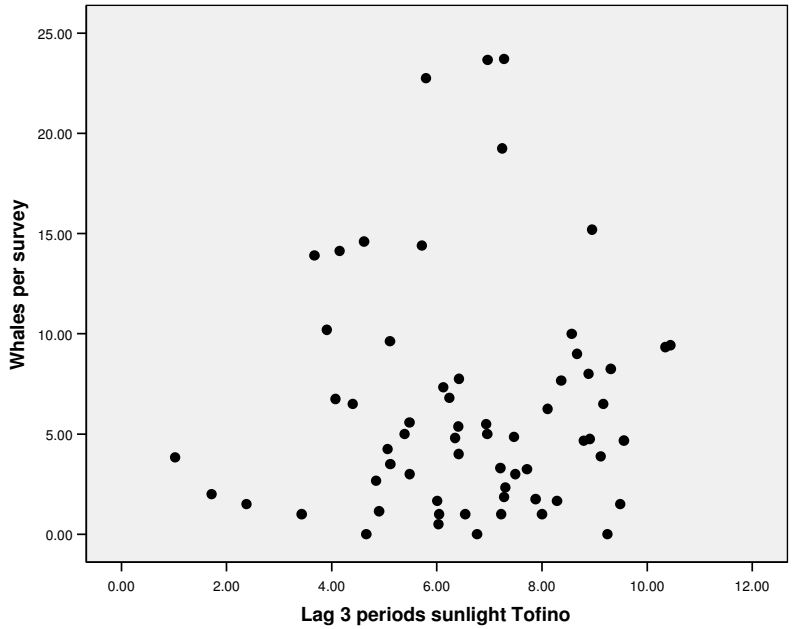
Lag 1 period sunlight Tofino vs. whales per survey



Lag 2 periods sunlight Tofino vs. whales per survey



Lag 3 periods sunlight Tofino vs. whales per survey



Lag 26 periods sunlight Tofino vs. whales per survey

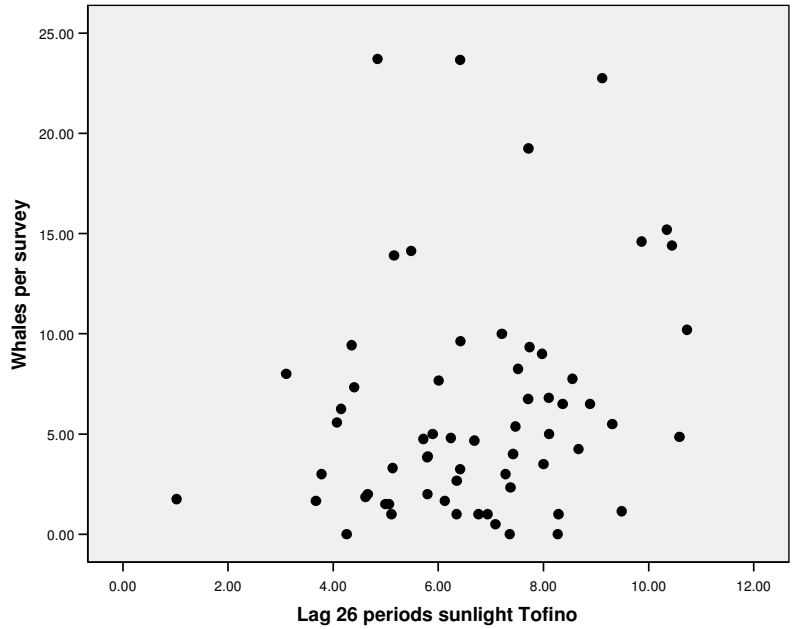
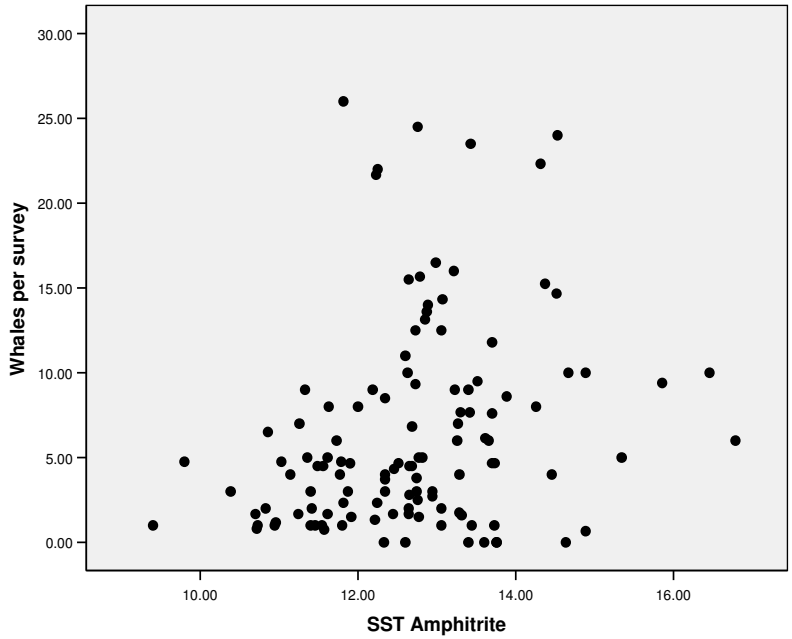
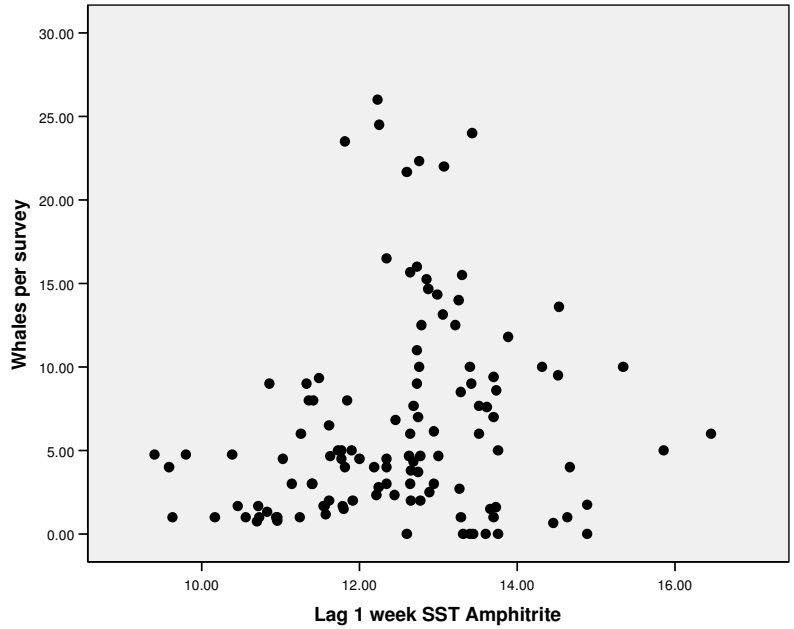


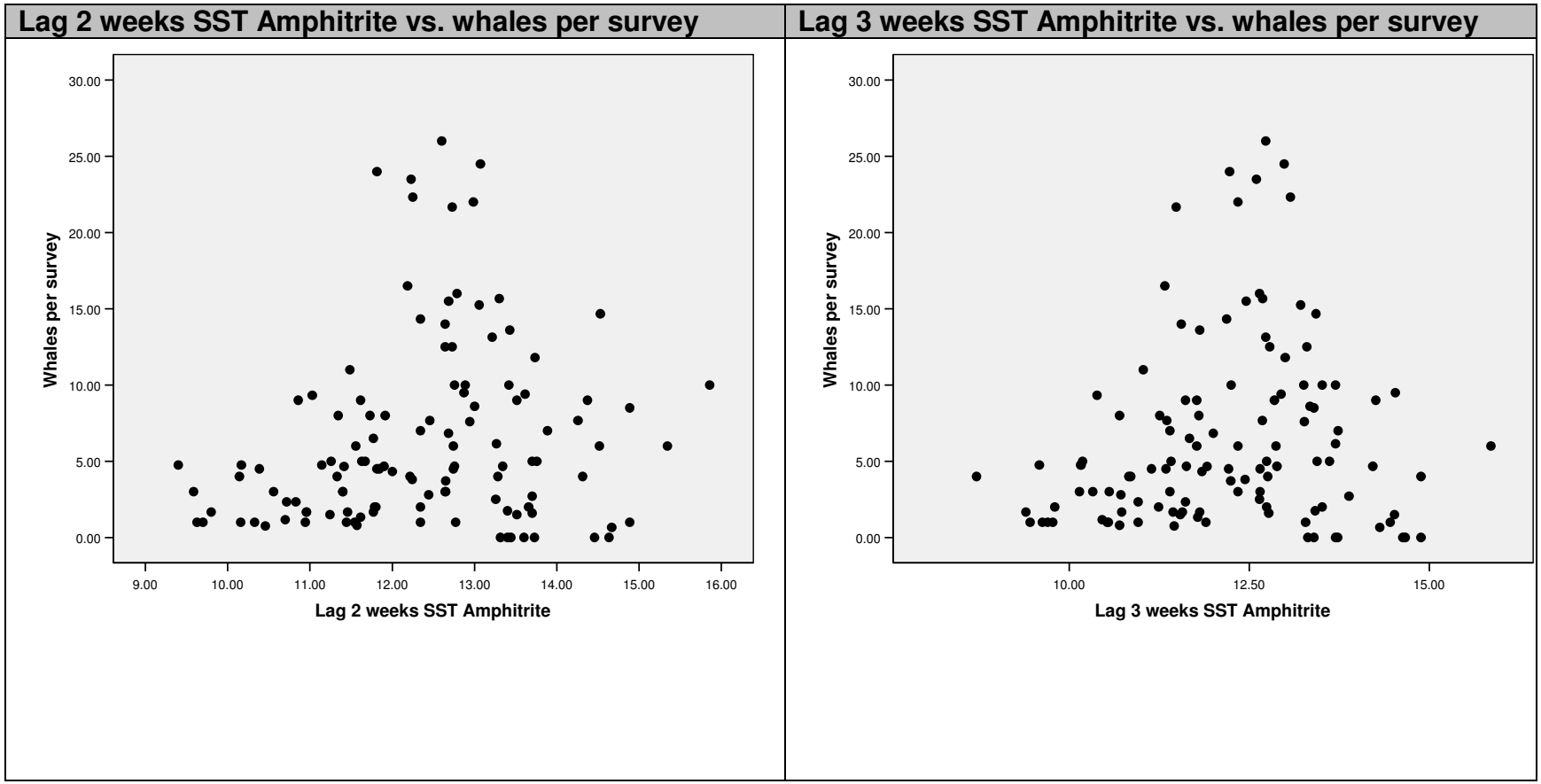
Figure 7. Scatterplots – weekly scale.

SST Amphitrite vs. whales per survey

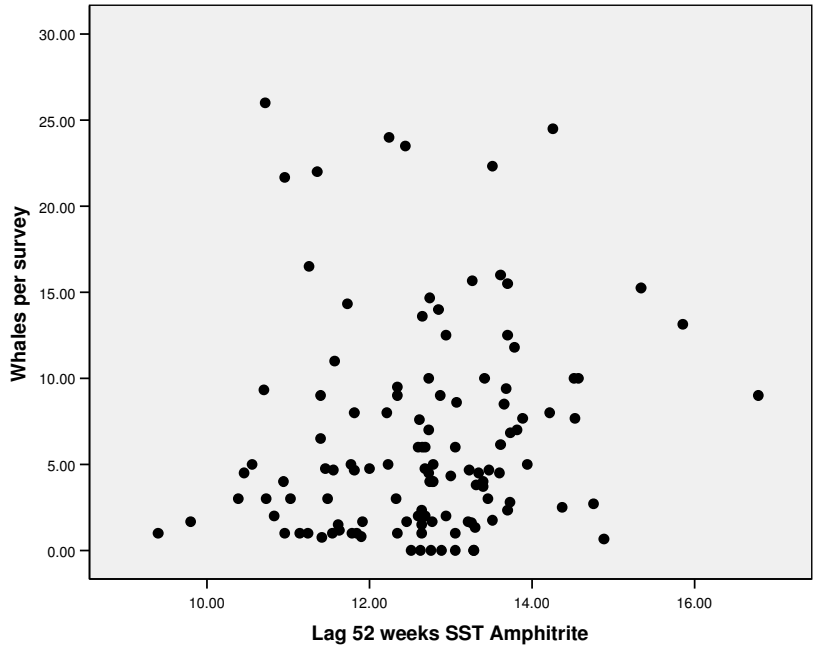


Lag 1 week SST Amphitrite vs. whales per survey

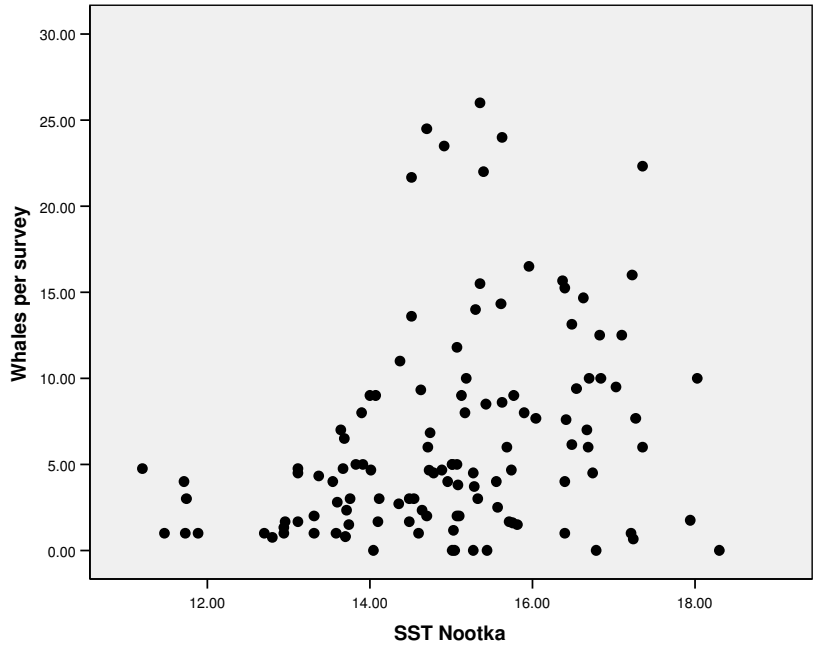



Lag 2 weeks SST Amphitrite vs. whales per survey
Whales per survey
30.00
25.00
20.00
15.00
10.00
5.00
0.00
9.00
10.00
11.00
12.00
13.00
14.00
15.00
16.00
Lag 2 weeks SST Amphitrite
Lag 3 weeks SST Amphitrite vs. whales per survey
Whales per survey
30.00
25.00
20.00
15.00
10.00
5.00
0.00
10.00
12.50
15.00
Lag 3 weeks SST Amphitrite

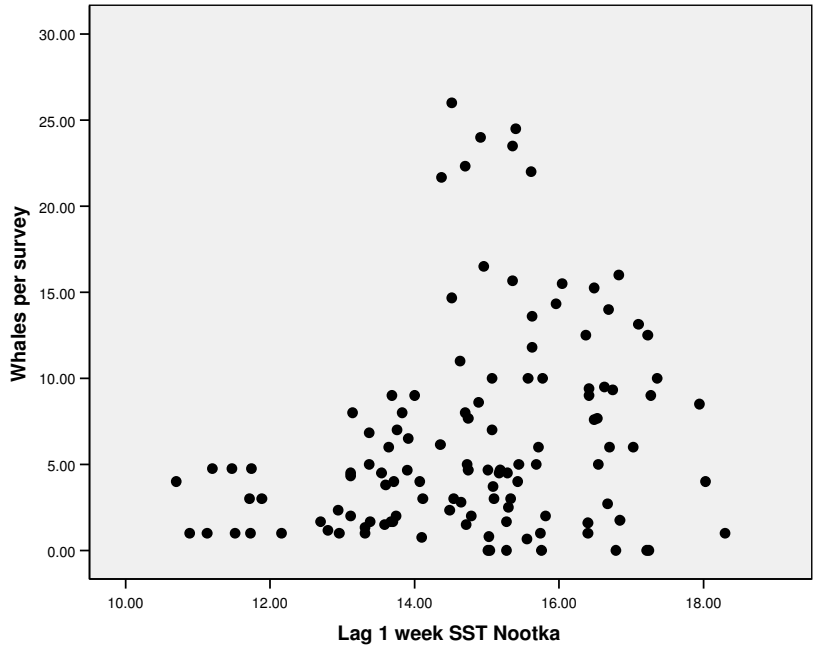
Lag 52 weeks SST Amphitrite vs. whales per survey



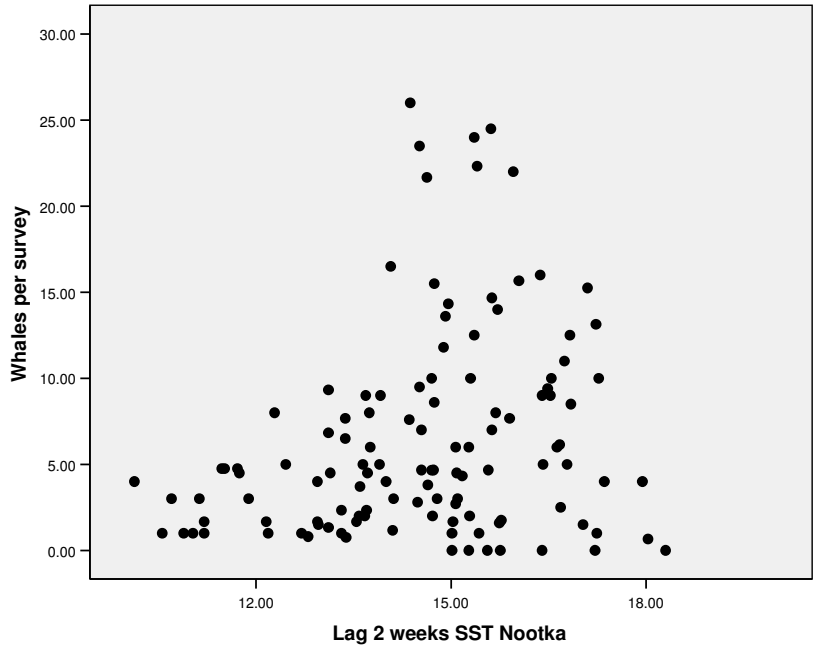
SST Nootka vs. whales per survey



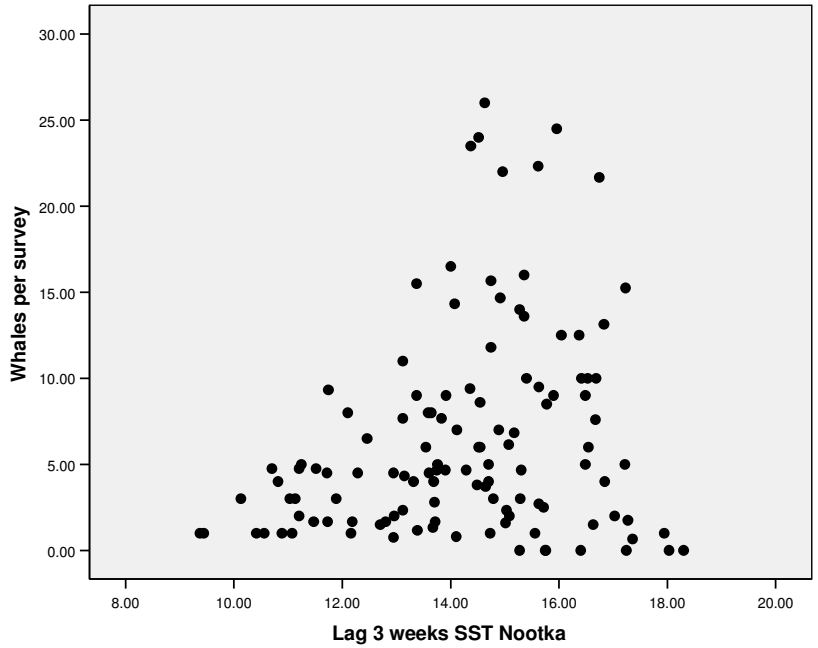
Lag 1 week SST Nootka vs. whales per survey



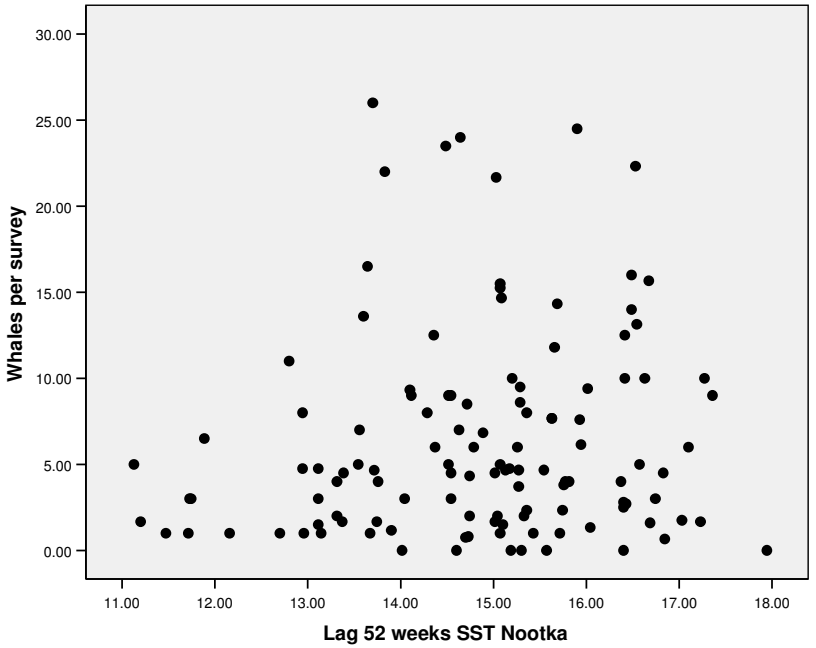
Lag 2 weeks SST Nootka vs. whales per survey



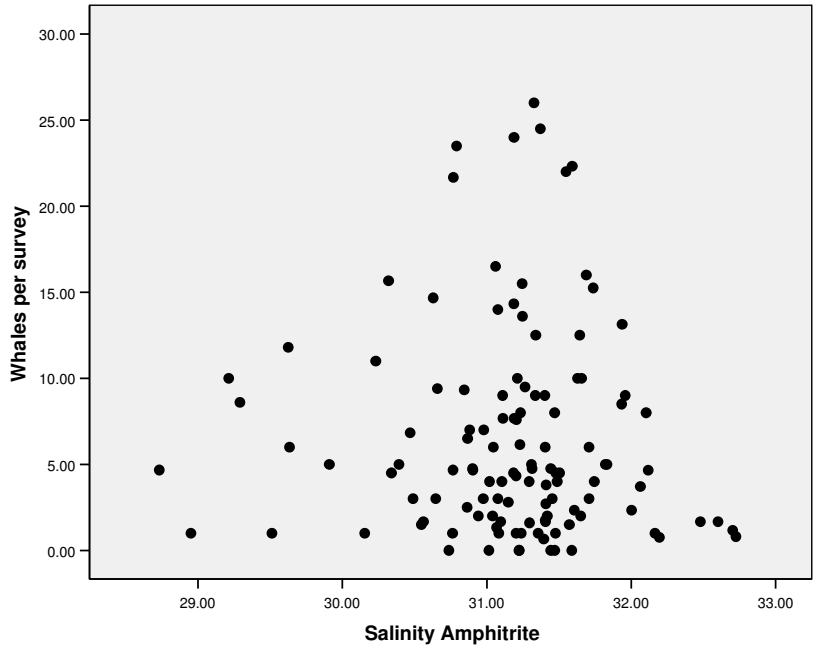
Lag 3 weeks SST Nootka vs. whales per survey



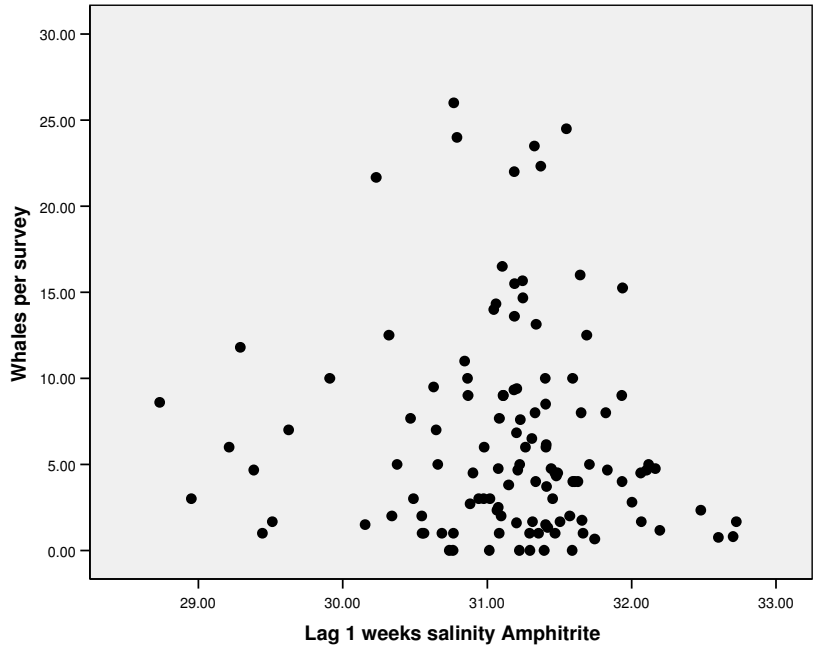
Lag 52 weeks SST Nootka vs. whales per survey



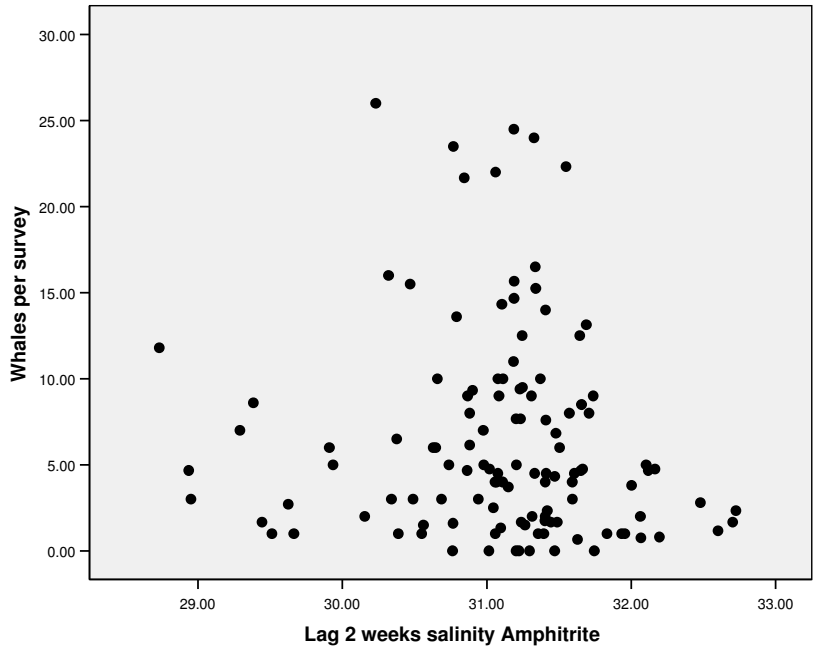
Salinity Amphitrite vs. whales per survey



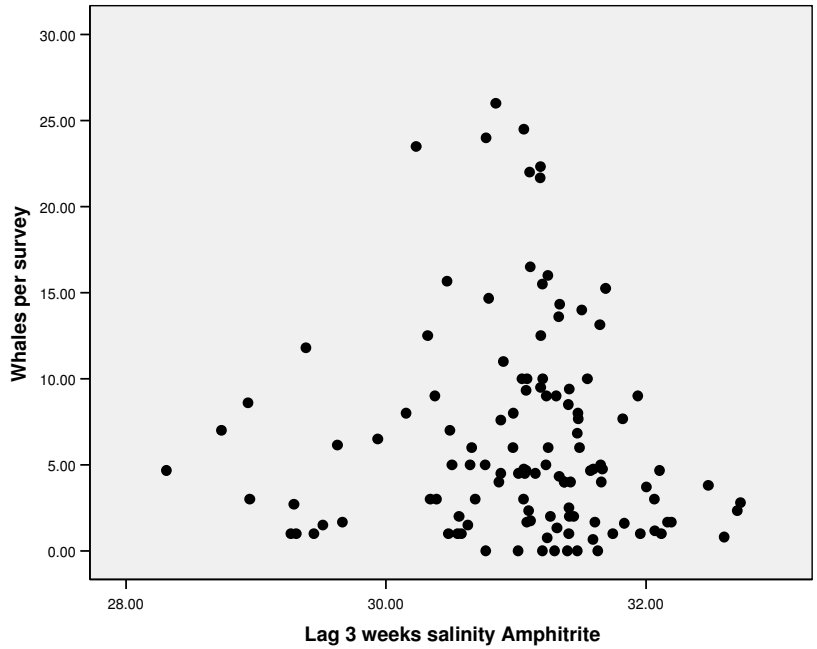
Lag 1 week salinity Amphitrite vs. whales per survey



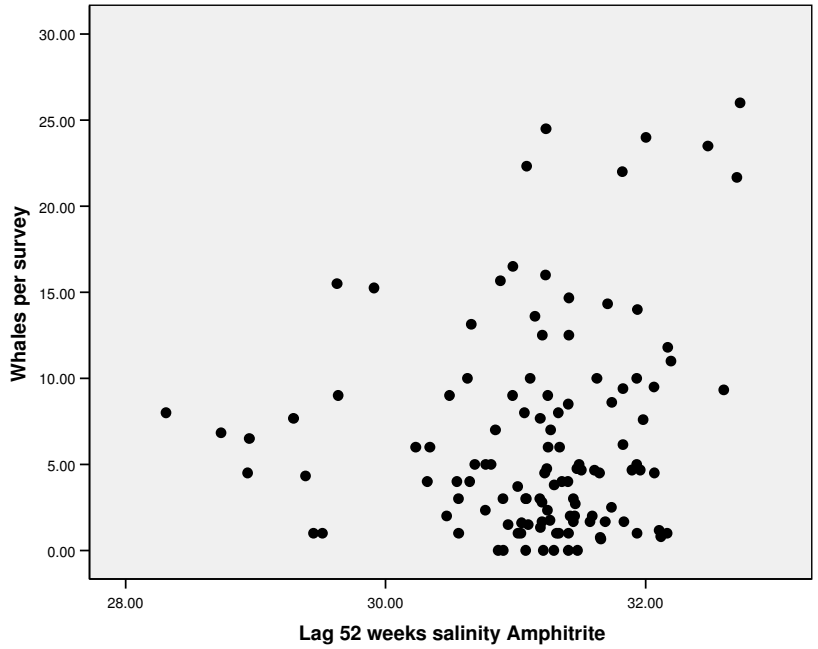
Lag 2 weeks salinity Amphitrite vs. whales per survey



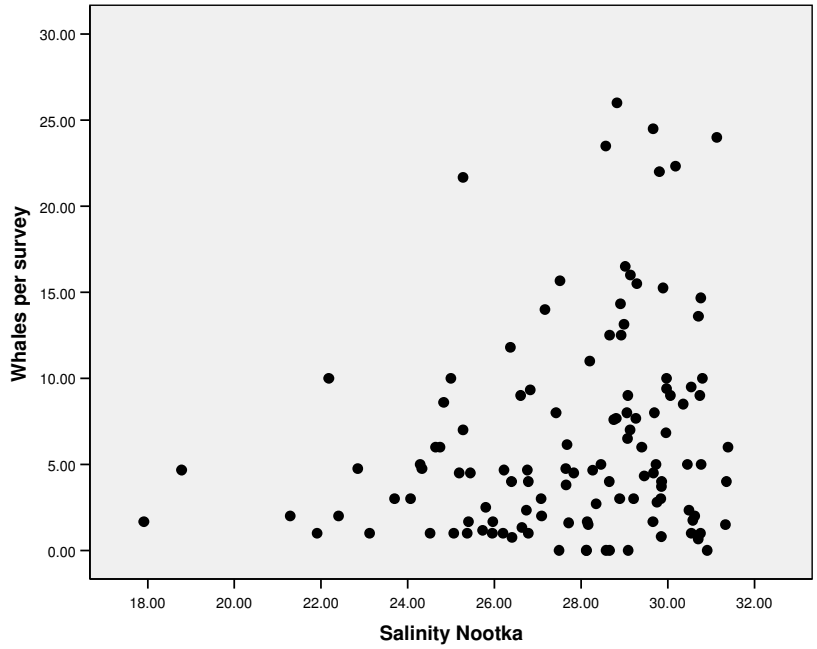
Lag 3 weeks salinity Amphitrite vs. whales per survey



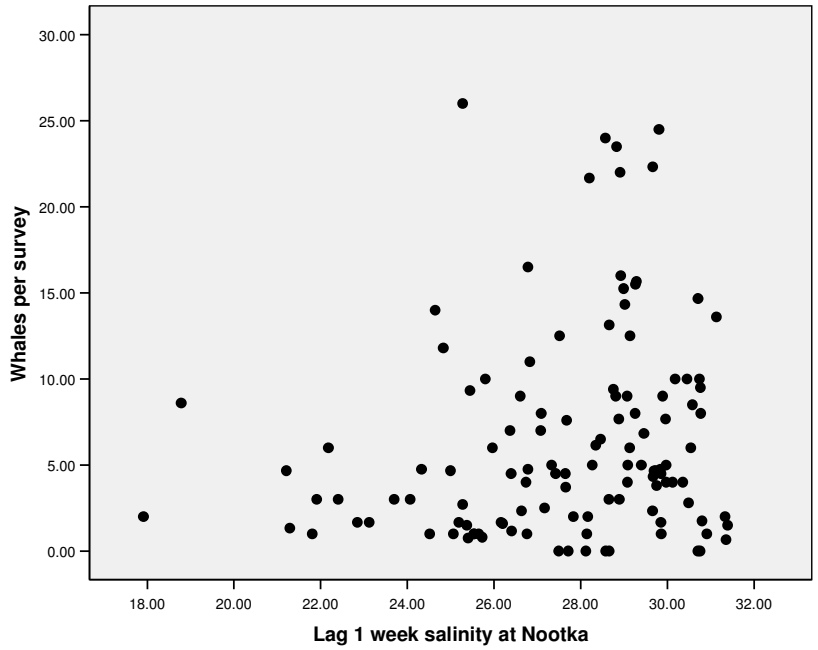
Lag 52 weeks salinity Amphitrite vs. whales per survey



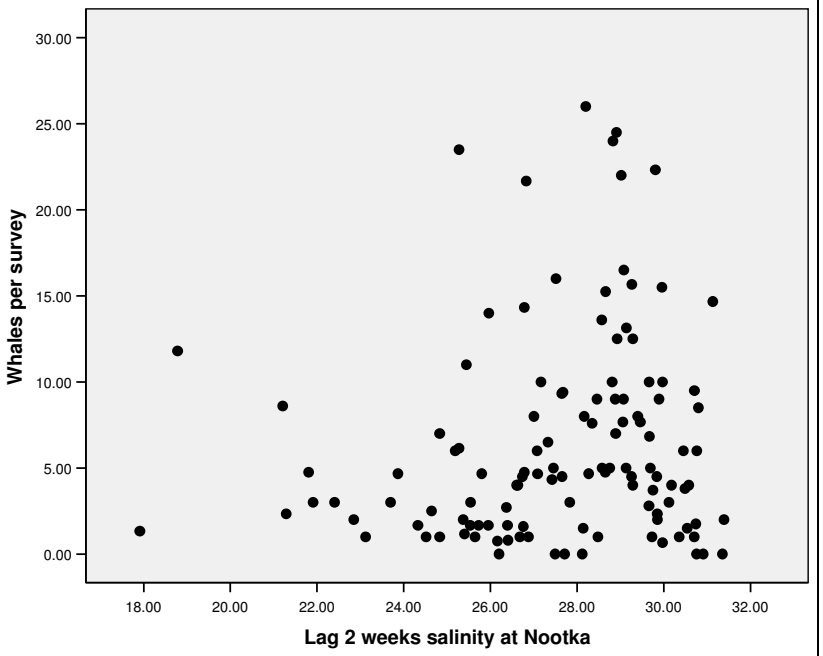
Salinity Nootka vs. whales per survey



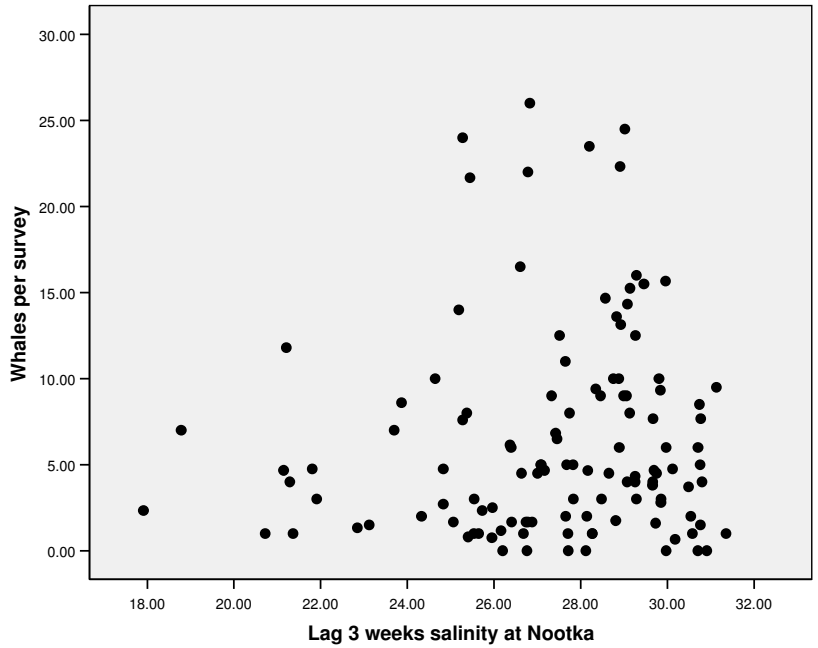
Lag 1 week salinity Nootka vs. whales per survey



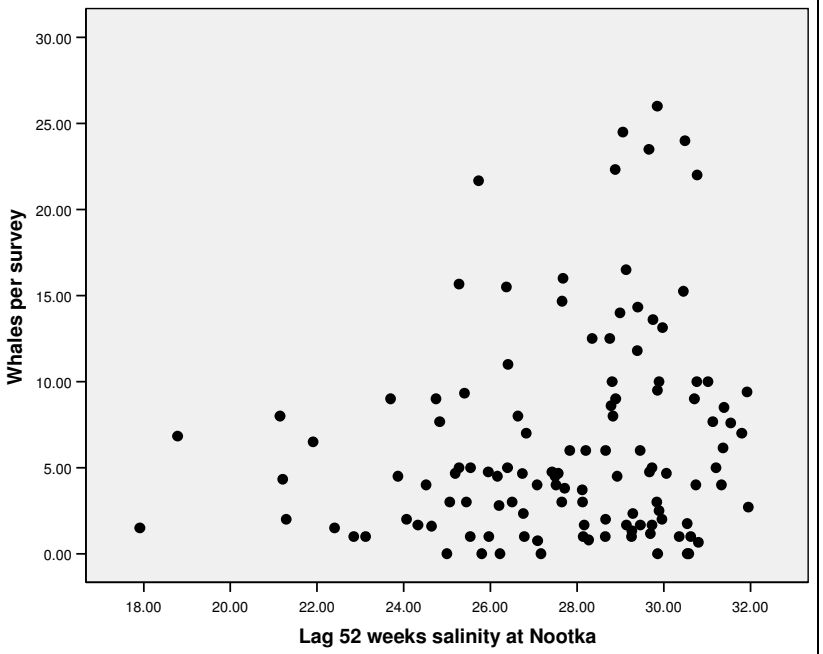
Lag 2 weeks salinity Nootka vs. whales per survey

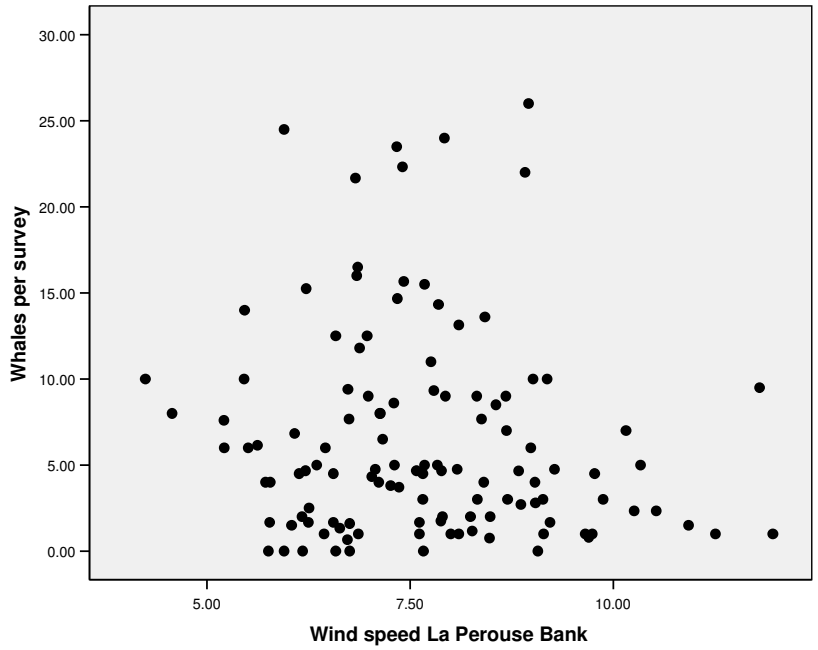
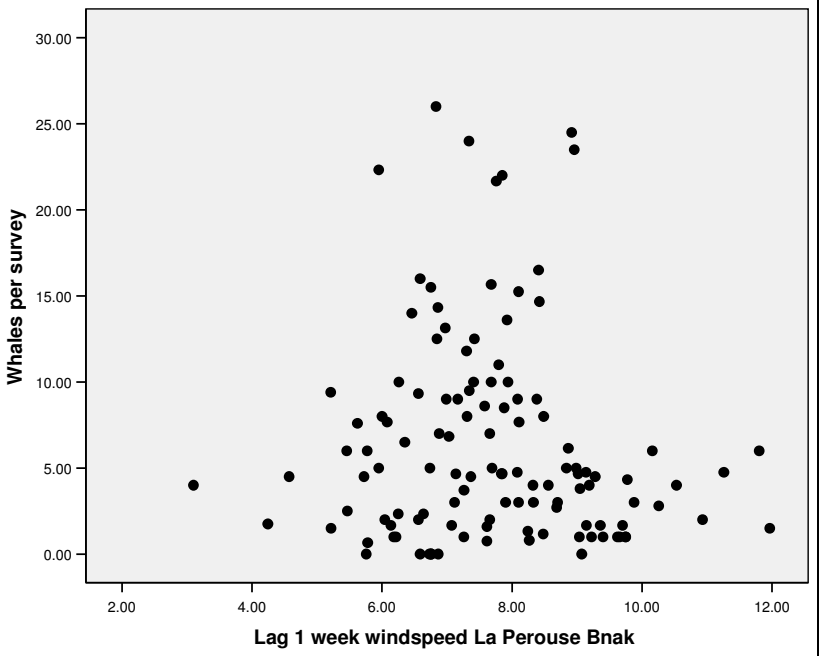


Lag 3 weeks salinity Nootka vs. whales per survey

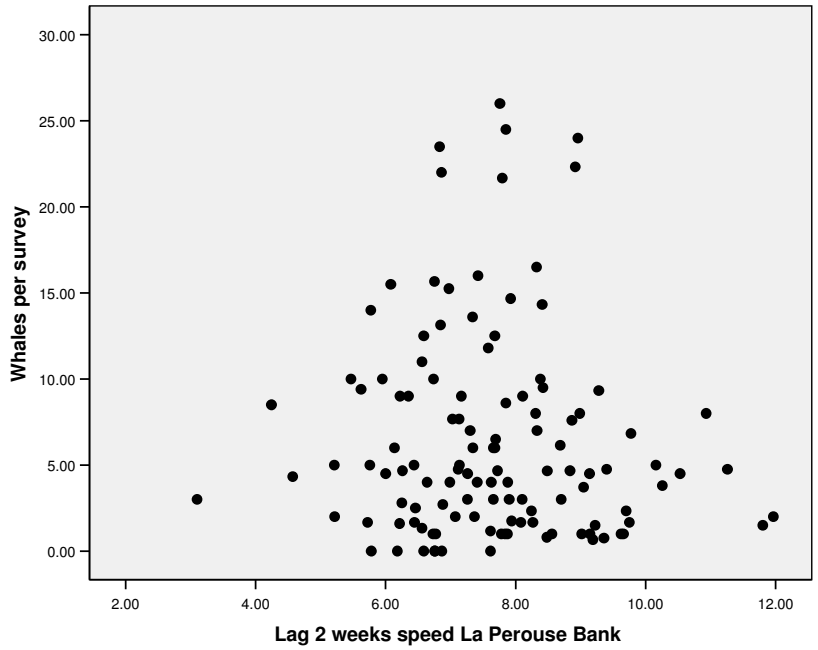


Lag 52 weeks salinity Nootka vs. whales per survey

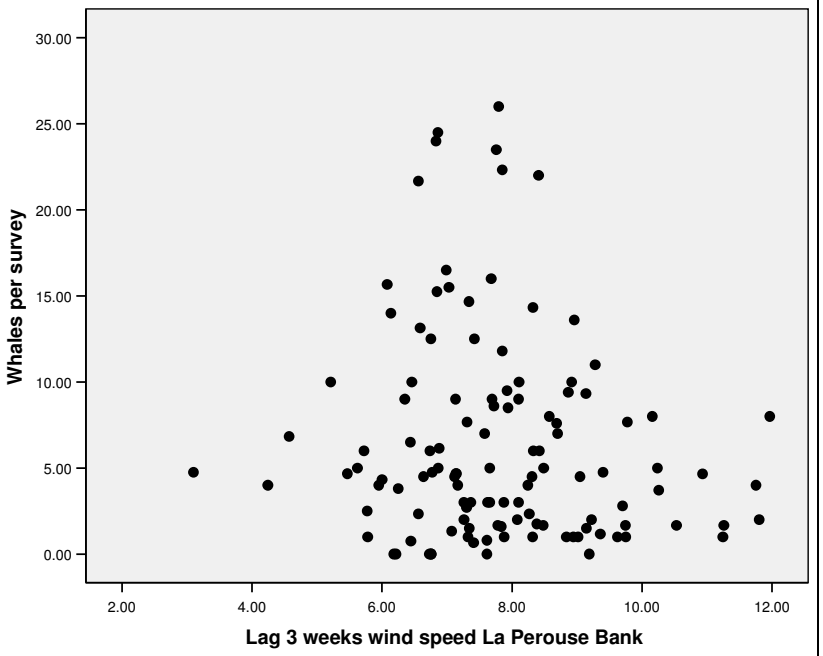


Wind speed La Perouse Bank vs. whales per survey	Lag 1 week wind speed La Perouse Bank vs. whales per survey
	

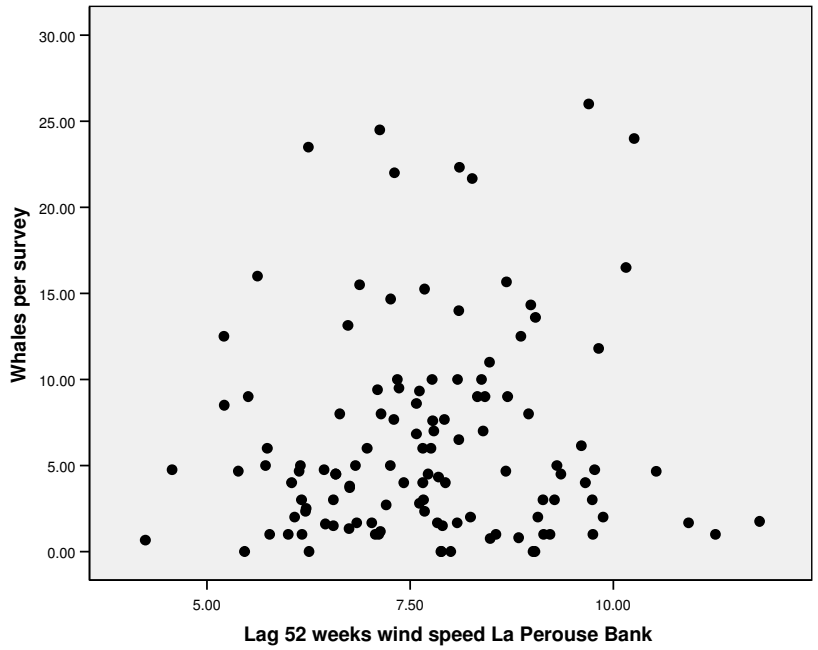
Lag 2 weeks wind speed La Perouse Bank vs. whales per survey



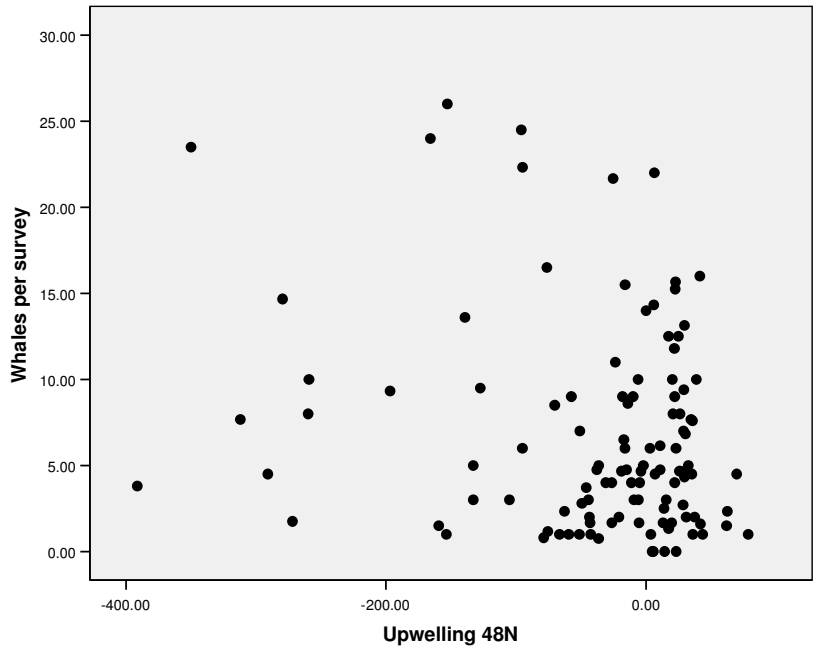
Lag 3 weeks wind speed La Perouse Bank vs. whales per survey



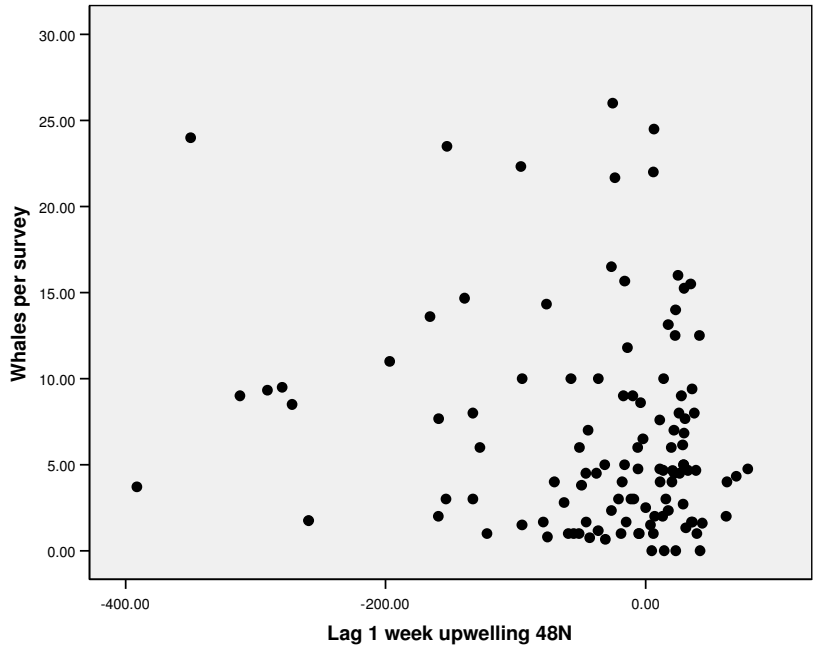
Lag 52 weeks wind speed La Perouse Bank vs. whales per survey



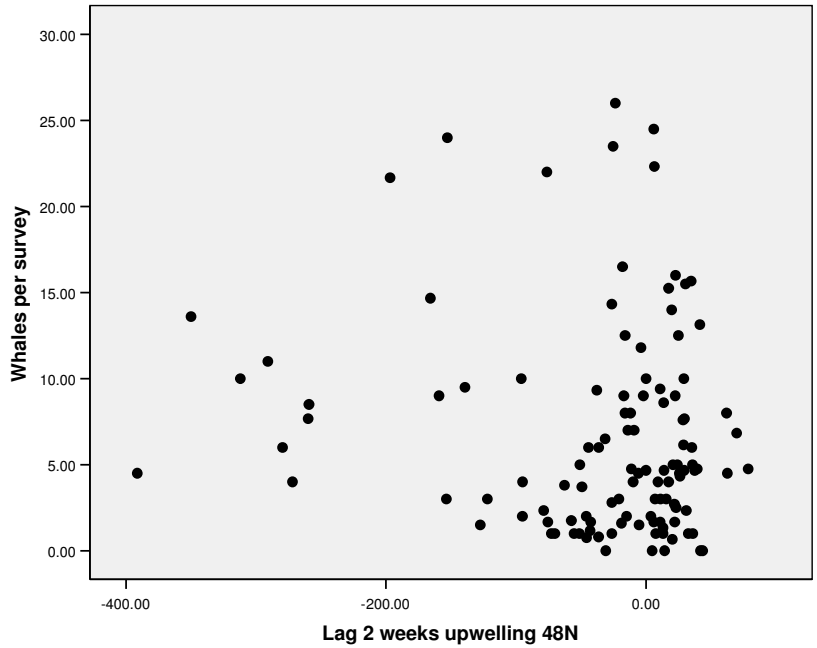
Upwelling 48N vs. whales per survey



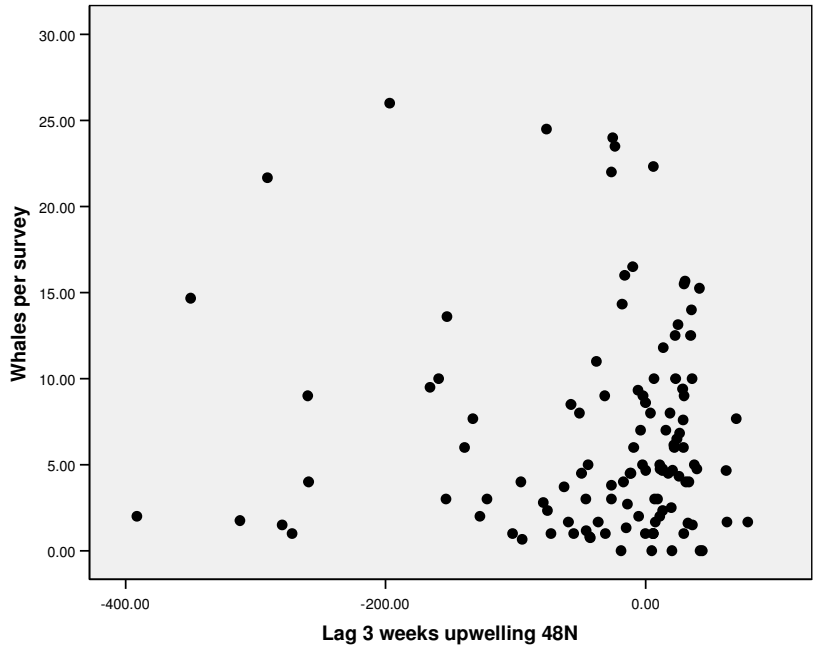
Lag 1 week upwelling 48N vs. whales per survey



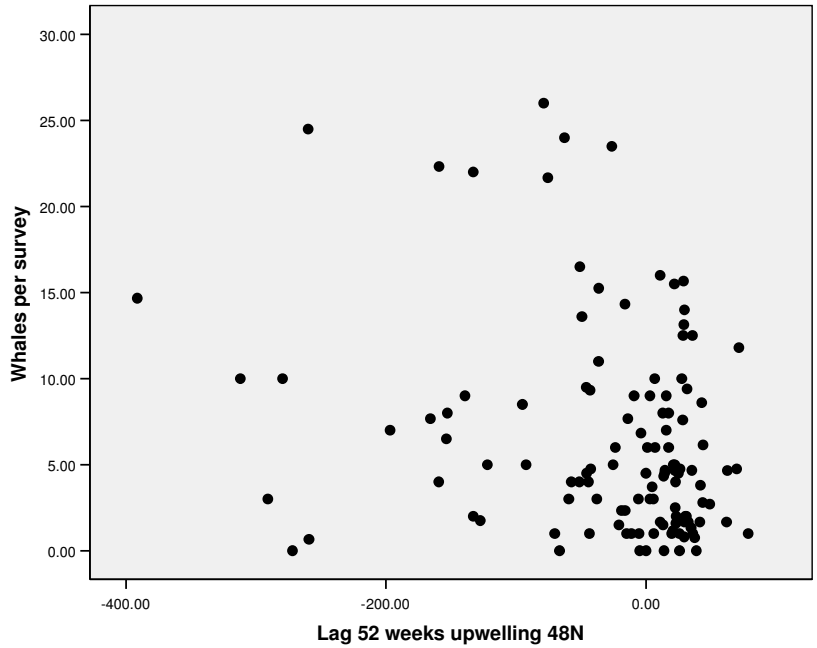
Lag 2 weeks upwelling 48N vs. whales per survey



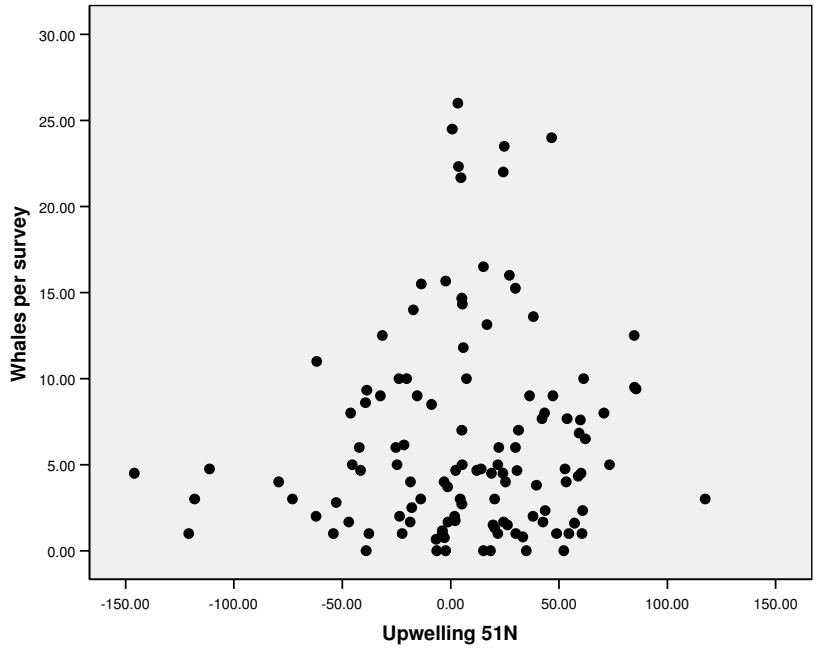
Lag 3 weeks upwelling 48N vs. whales per survey



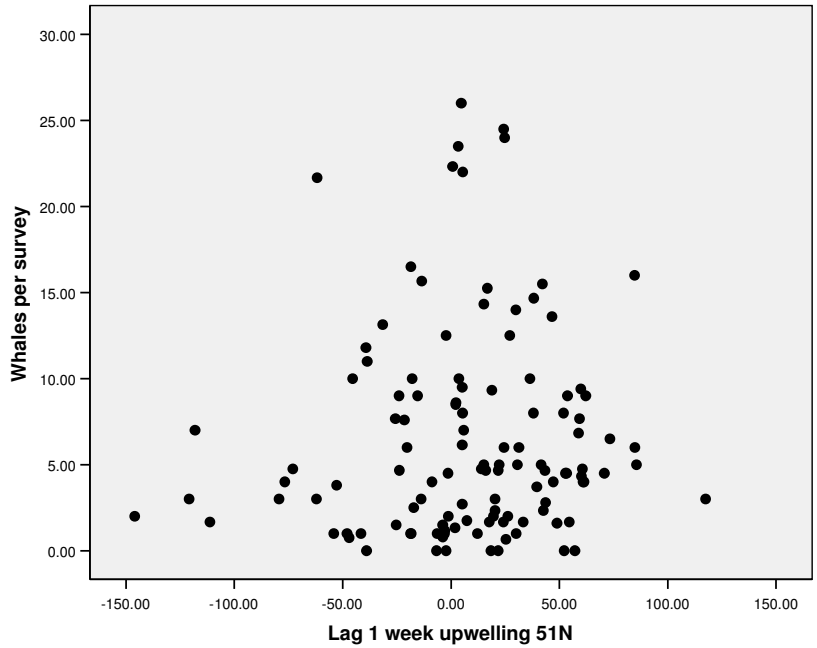
Lag 52 weeks upwelling 48N vs. whales per survey



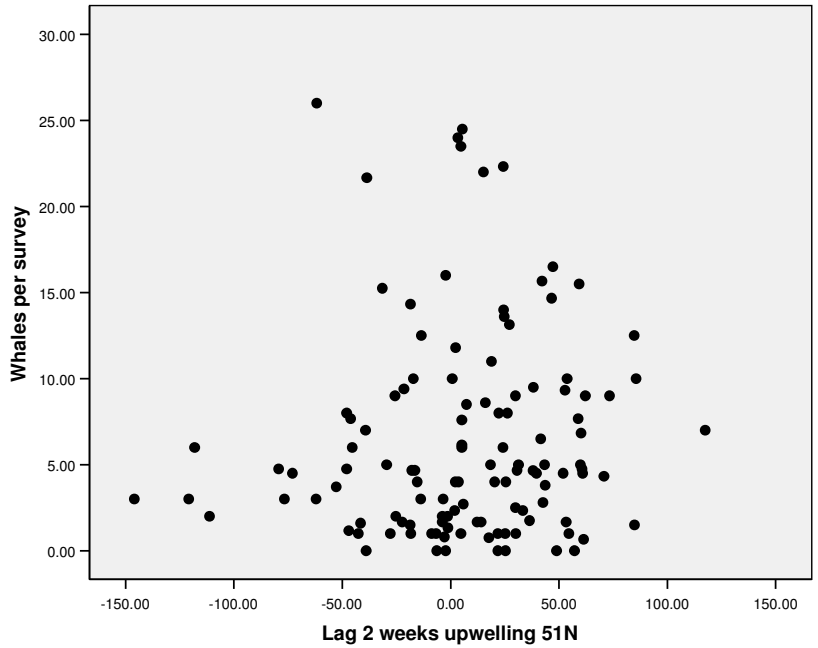
Upwelling 51N vs. whales per survey



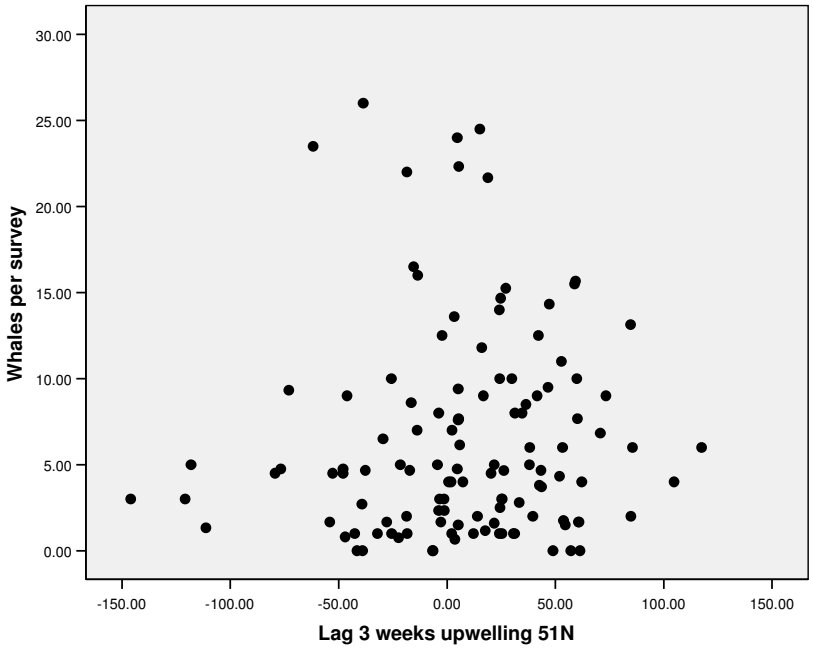
Lag 1 week upwelling 51N vs. whales per survey



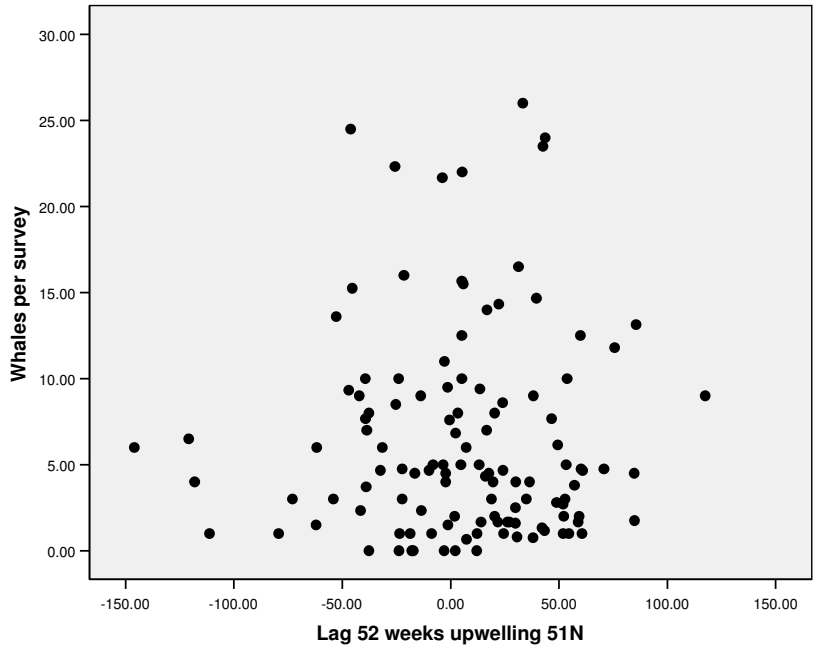
Lag 2 weeks upwelling 51N vs. whales per survey



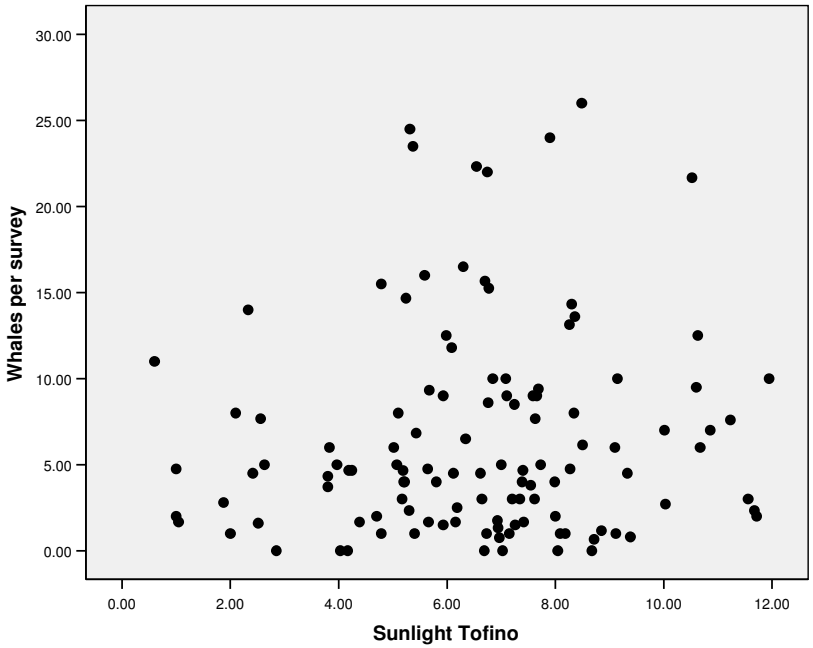
Lag 3 weeks upwelling 51N vs. whales per survey

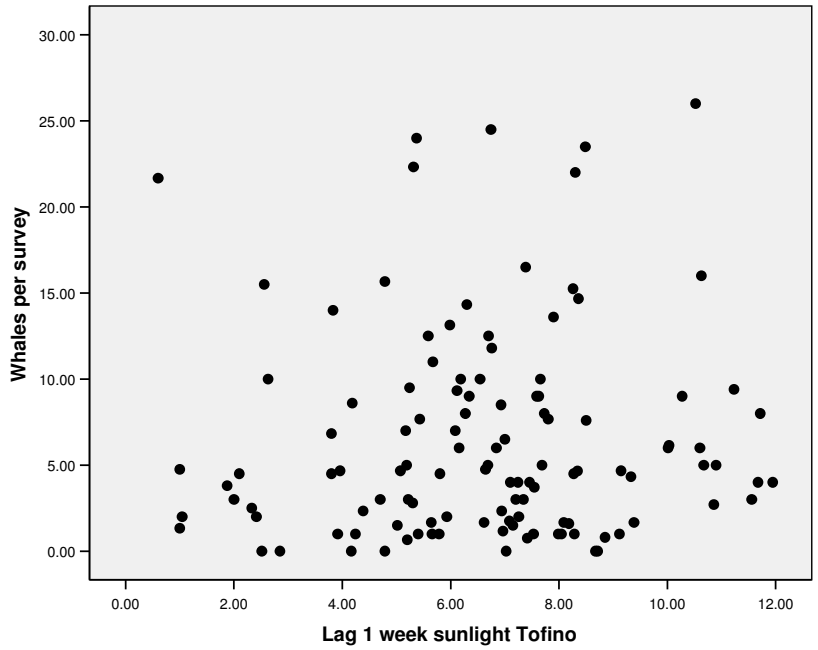
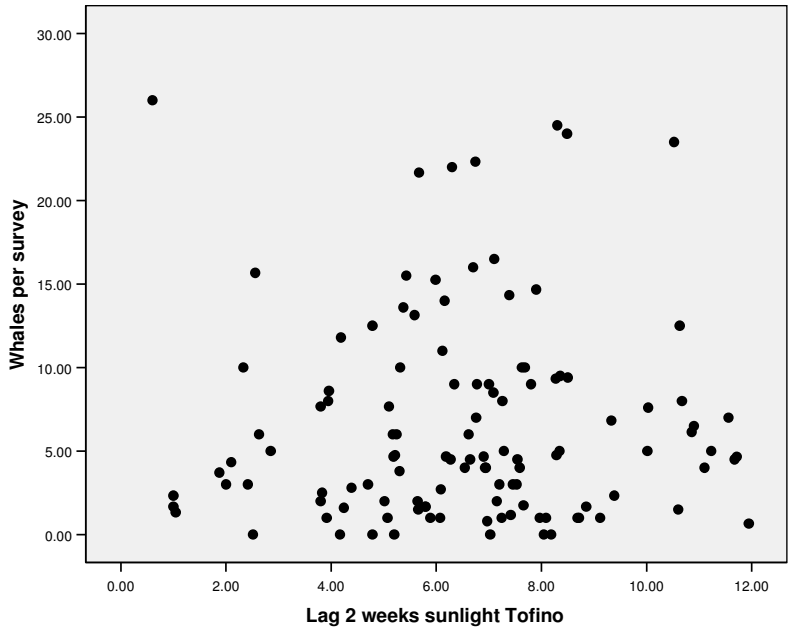


Lag 52 weeks upwelling 51N vs. whales per survey

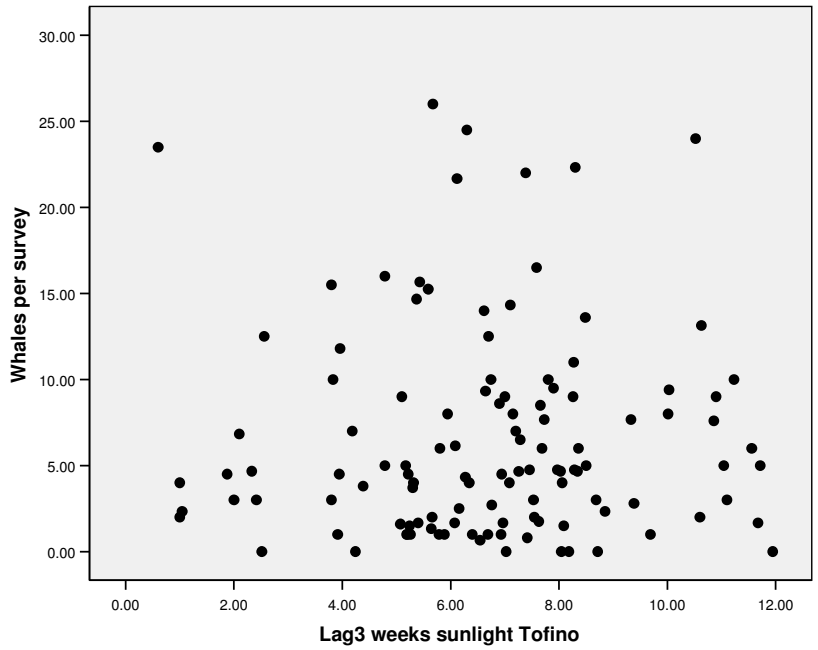


Sunlight Tofino vs. whales per survey

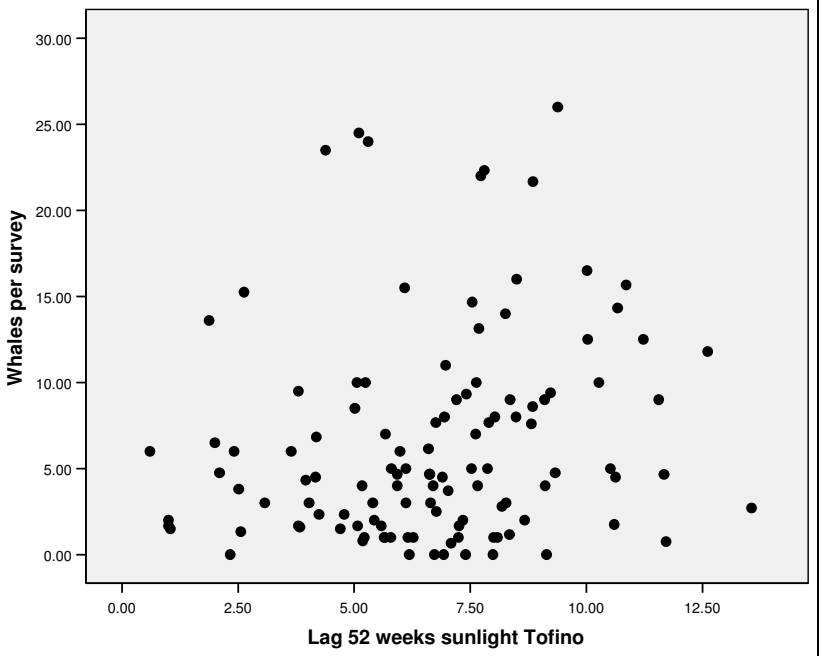


Lag 1 week sunlight Tofino vs. whales per survey	Lag 2 weeks sunlight Tofino vs. whales per survey
	

Lag 3 weeks sunlight Tofino vs. whales per survey



Lag 52 weeks sunlight Tofino vs. whales per survey



Appendix II. Komolgorov-Smirnov tests.

	Whales per survey	Lag 1 year whales per survey	Lag 2 year whales per survey	SST Amphitrite	Lag 1 year SST Amphitrite	Lag 2 years SST Amphitrite	SST Nootka	Lag 1 year SST Nootka
N	8	7	6	10	9	8	10	9
Kolmogorov-Smirnov Z	.384	.417	.531	.518	.523	.582	.374	.416
Asymp. Sig. (2-tailed)	.998	.995	.941	.952	.947	.887	.999	.995

	Lag 2 years SST Nootka	Salinity Amphitrite	Lag 1 year salinity Amphitrite	Lag 2 years salinity Amphitrite	Salinity Nootka	Lag 1 year salinity Nootka	Lag 2 years salinity Nootka	Wind speed La Perouse Bank
N	8	10	9	8	10	9	8	10
Kolmogorov-Smirnov Z	.436	.594	.487	.623	.915	.957	.844	.504
Asymp. Sig. (2-tailed)	.991	.872	.972	.832	.373	.319	.475	.961

	Lag 1 year wind speed	Lag 2 years wind speed	Upwelling 48N	Lag 1 year upwelling 48N	Lag 2 years upwelling 48N	Upwelling 51N	Lag 1 year upwelling 51N	Lag 2 years upwelling 51N
N	9	8	10	9	8	10	9	8
Kolmogorov-Smirnov Z	.597	.562	.677	.552	.586	.413	.447	.500
Asymp. Sig. (2-tailed)	.868	.911	.749	.921	.883	.996	.988	.964

	Sunlight Tofino	Lag 1 year sunlight	Lag 2 years sunlight	Upwelling 45N	Lag 1 year upwelling 45N	Lag 2 years upwelling 45N	Upwelling 42N	Lag 1 year upwelling 42N
N	10	9	8	10	9	8	10	9
Kolmogorov-Smirnov Z	.696	.598	.588	.413	.420	.545	.518	.448
Asymp. Sig. (2-tailed)	.719	.867	.880	.996	.994	.927	.951	.988

	Lag 2 upwelling 42N	Upwelling 54N	Lag 1 year upwelling 54N	Lag 2 years upwelling 54N	Year	Year variables
N	8	10	9	8	10	10
Kolmogorov-Smirnov Z	.423	.729	.768	.685	0.302	1.657
Asymp. Sig. (2-tailed)	.994	.662	.596	.736	1.000	.008

Table 11. One sample Komolgorov-Smirnov tests for data aggregated at a yearly scale, by variable. Significances indicating normal distributions are highlighted in grey, while significances indicating non-normal distributions are highlighted in pink.

	Whales per survey	Lag 1 month whales per survey	Lag 2 months whales per survey	Lag 3 months whales per survey	Lag 12 months whales per survey	SST Amphitrite	Lag 1 month SST Amphitrite	Lag 2 months SST Amphitrite
N	36	36	36	36	31	120	119	118
Kolmogorov-Smirnov Z	.825	.825	.825	.825	.736	.907	.878	.914
Asymp. Sig. (2-tailed)	.505	.505	.505	.505	.651	.383	.424	.374

	Lag 3 months SST Amphitrite	Lag 12 months SST Amphitrite	SST Nootka	Lag 1 month SST Nootka	Lag 2 months SST Nootka	Lag 3 months SST Nootka	Lag 12 months SST Nootka	Salinity at Amphitrite
N	117	108	120	119	118	117	108	120
Kolmogorov-Smirnov Z	.924	.907	1.395	1.360	1.395	1.405	1.328	1.454
Asymp. Sig. (2-tailed)	.361	.383	.041	.049	.041	.039	.059	.029

	Lag 1 month salinity Amphitrite	Lag 2 months salinity Amphitrite	Lag 3 months salinity Amphitrite	Lag of 12 months salinity Amphitrite	Salinity Nootka	Lag 1 month salinity Nootka	Lag 2 months salinity Nootka	Lag 3 months salinity Nootka
N	119	118	117	108	120	119	118	117
Kolmogorov-Smirnov Z	1.453	1.451	1.470	1.473	.523	.543	.537	.535
Asymp. Sig. (2-tailed)	.029	.030	.027	.026	.947	.930	.935	.937

	Lag 12 months salinity Nootka	Wind speed La Perouse Bank	Lag 1 month wind speed	Lag 2 months wind speed	Lag 3 months wind speed	Lag 12 months wind speed	Upwelling 48N	Lag 1 month upwelling 48N
N	108	120	119	118	117	108	120	119
Kolmogorov-Smirnov Z	.551	.950	.954	.965	.999	.917	1.651	1.672
Asymp. Sig. (2-tailed)	.922	.328	.322	.310	.271	.370	.009	.007

	Lag 2 months upwelling 48N	Lag 3 months upwelling 48N	Lag 12 months upwelling 48N	Upwelling 51 N	Lag 1 month upwelling 51N	Lag 2 months upwelling 51N	Lag 3 months upwelling 51N	Lag 12 months upwelling 51N
N	118	117	108	120	119	118	117	108
Kolmogorov-Smirnov Z	1.704	1.741	1.569	1.095	1.062	1.039	1.011	.971
Asymp. Sig. (2-tailed)	.006	.005	.015	.182	.210	.231	.258	.303

	Sunlight Tofino	Lag 1 month sunlight	Lag 2 months sunlight	Lag 3 months sunlight	Lag 12 months sunlight	Dummy variable - month
N	120	119	118	117	108	120
Kolmogorov-Smirnov Z	.953	.948	.946	.952	.973	5.857
Asymp. Sig. (2-tailed)	.324	.330	.332	.325	.300	.000

Table 12. One sample Komolgorov-Smirnov tests for data aggregated at a monthly scale, by variable. Significances indicating normal distributions are highlighted in grey, while significances indicating non-normal distributions are highlighted in pink.

	SST Amphitrite	Lag 1 period SST Amphitrite	Lag 2 periods SST Amphitrite	Lag 3 periods SST Amphitrite	Lag 26 periods SST Amphitrite	SST Nootka	Lag 1 period SST Nootka	Lag 2 periods SST Nootka
N	260	260	260	260	260	260	260	260
Kolmogorov-Smirnov Z	1.496	1.496	1.496	1.496	1.496	1.840	1.840	1.840
Asymp. Sig. (2-tailed)	.023	.023	.023	.023	.023	.002	.002	.002

	Lag 3 periods SST Nootka	Lag 26 periods SST Nootka	Salinity at Amphitrite	Lag 1 period salinity Amphitrite	Lag 2 periods salinity Amphitrite	Lag 3 periods salinity Amphitrite	Lag 26 periods salinity Amphitrite	Salinity Nootka
N	260	260	260	260	260	260	260	260
Kolmogorov-Smirnov Z	1.840	1.840	1.980	1.980	1.980	1.980	1.980	.837
Asymp. Sig. (2-tailed)	.002	.002	.001	.001	.001	.001	.001	.486

	Lag 1 period salinity Nootka	Lag 2 periods salinity Nootka	Lag 3 periods salinity Nootka	Lag 26 periods salinity Nootka	Wind speed La Perouse Bank	Lag 1 period wind speed	Lag 2 periods wind speed	Lag 3 periods wind speed
N	260	260	260	260	250	250	250	250
Kolmogorov-Smirnov Z	.837	.837	.837	.837	1.341	1.341	1.341	1.341
Asymp. Sig. (2-tailed)	.486	.486	.486	.486	.055	.055	.055	.055

	Lag 26 periods wind speed	Upwelling 48N	Lag 1 period upwelling 48N	Lag 2 periods upwelling 48N	Lag 3 periods upwelling 48N	Lag 26 periods upwelling 48N	Upwelling 51N	Lag 1 period upwelling 51N
N	250	260	260	260	260	260	260	259
Kolmogorov-Smirnov Z	1.341	2.710	2.710	2.710	2.710	2.710	1.859	1.852
Asymp. Sig. (2-tailed)	.055	.000	.000	.000	.000	.000	.002	.002

	Lag 2 periods upwelling 51N	Lag 3 periods upwelling 51N	Lag 26 periods upwelling 51N	Sunlight at Tofino	Lag 1 period sunlight	Lag 2 periods sunlight	Lag 3 periods sunlight	Lag 26 periods sunlight
N	258	257	234	258	257	256	255	232
Kolmogorov-Smirnov Z	1.874	1.871	1.777	1.268	.790	1.236	1.204	1.183
Asymp. Sig. (2-tailed)	.002	.002	.004	.080	.091	.094	.110	.122

	Year	Year variables	Semi-month period	Period number variables	Whales per survey	Lag 1 period whales per survey	Lag 2 periods whales per survey	Lag 3 periods whales per survey
N	260	260	260	260	64	64	64	64
Kolmogorov-Smirnov Z	1.733	8.551	1.221	8.718	1.238	1.238	1.238	1.238
Asymp. Sig. (2-tailed)	.005	.000	.101	.000	.093	.093	.093	.093

	Lag 26 periods whales per survey	Year
N	64	260
Kolmogorov-Smirnov Z	1.238	1.733
Asymp. Sig. (2-tailed)	.093	.005

Table 13. One sample Komolgorov-Smirnov tests for data aggregated at a semi-monthly scale, by variable. Significances indicating normal distributions are highlighted in grey, while significances indicating non-normal distributions are highlighted in pink.

	Year	Week	Whales per survey	Lag 1 week whales per surveys	Lag 2 weeks whales per survey	Lag 3 weeks whales per survey	Lag 52 weeks whales per survey	Year variables
N	520	520	119	119	119	119	101	520
Kolmogorov-Smirnov Z	2.457	1.517	1.969	1.969	1.969	1.969	1.784	12.096
Asymp. Sig. (2-tailed)	.000	.020	.001	.001	.001	.001	.003	.000

	Week variables	SST at Amphitrite	Lag 1 week SST Amphitrite	Lag 2 weeks SST Amphitrite	Lag 3 weeks SST Amphitrite	Lag 52 weeks SST Amphitrite	SST at Nootka	Lag 1 week SST Nootka
N	520	520	519	518	517	468	520	519
Kolmogorov-Smirnov Z	12.232	1.647	1.638	1.620	1.601	1.574	2.397	2.381
Asymp. Sig. (2-tailed)	.000	.009	.009	.011	.012	.014	.000	.000

	Lag 2 weeks SST Nootka	Lag 3 weeks SST Nootka	Lag 52 weeks SST Nootka	Salinity Amphitrite	Lag 1 weeks salinity Amphitrite	Lag 2 weeks salinity Amphitrite	Lag 3 weeks salinity Amphitrite	Lag 52 weeks salinity Amphitrite
N	518	517	468	520	519	518	517	468
Kolmogorov-Smirnov Z	2.362	2.341	2.281	2.223	2.220	2.222	2.226	2.157
Asymp. Sig. (2-tailed)	.000	.000	.000	.000	.000	.000	.000	.000

	Salinity Nootka	Lag 1 week salinity Nootka	Lag 2 weeks salinity Nootka	Lag 3 weeks salinity Nootka	Lag 52 weeks salinity Nootka	Wind speed La Perouse Bank	Lag 1 week wind speed	Lag 2 weeks wind speed
N	520	519	518	517	468	495	494	493
Kolmogorov-Smirnov Z	1.142	1.156	1.150	1.150	1.164	1.463	1.443	1.454
Asymp. Sig. (2-tailed)	.147	.138	.142	.136	.133	.028	.031	.029

	Lag 3 weeks wind speed	Lag 52 weeks wind speed	Upwelling 48N	Lag 1 weeks upwelling 48N	Lag 2 weeks upwelling at 48N	Lag 3 weeks upwelling 48N	Lag 52 weeks upwelling 48N	Upwelling 51N
N	492	443	520	519	518	517	468	520
Kolmogorov-Smirnov Z	1.454	1.469	3.680	3.704	3.696	3.706	3.436	2.213
Asymp. Sig. (2-tailed)	.029	.027	.000	.000	.000	.000	.000	.000

	Lag 1 week upwelling 51N	Lag 2 weeks upwelling 51N	Lag 3 weeks upwelling 51N	Lag 52 weeks upwelling 51N	Sunlight Tofino	Lag 1 week sunlight	Lag 2 week sunlight	Lag 3 weeks sunlight
N	519	518	517	468	514	513	512	511
Kolmogorov-Smirnov Z	2.202	2.186	2.193	2.137	1.705	1.684	1.666	1.656
Asymp. Sig. (2-tailed)	.000	.000	.000	.000	.006	.007	.008	.008

	Lag 52 weeks sunlight
N	462
Kolmogorov-Smirnov Z	1.787
Asymp. Sig. (2-tailed)	.003

Table 14. One sample Komolgorov-Smirnov tests for data aggregated at a weekly scale, by variable. Significances indicating normal distributions are highlighted in grey, while significances indicating non-normal distributions are highlighted in pink.

Appendix III. Regression results – single regressions.

Variable	R^2	Sig.
SST Amphitrite	0.068	0.004
Lag 1 week SST Amphitrite	0.029	0.063
Lag 2 weeks SST Amphitrite	0.034	0.045
Lag 3 weeks SST Amphitrite	0.019	0.133
Lag 52 weeks SST Amphitrite	0.015	0.184
SST Nootka	0.097	0.001
Lag 1 week SST Nootka	0.063	0.006
Lag 2 weeks SST Nootka	0.060	0.007
Lag 3 weeks SST Nootka	0.051	0.013
Lag 52 weeks SST Nootka	0.015	0.188
Salinity Amphitrite	0.03	0.585
Lag 1 week salinity Amphitrite	0.007	0.386
Lag 2 weeks salinity Amphitrite	0.010	0.272
Lag 3 weeks salinity Amphitrite	0.004	0.496
Lag 52 weeks salinity Amphitrite	0.021	0.112
Salinity Nootka	0.054	0.011
Lag 1 week salinity Nootka	0.033	0.050
Lag 2 weeks salinity Nootka	0.020	0.129
Lag 3 weeks salinity Nootka	0.006	0.394
Lag 52 weeks salinity Nootka	0.037	0.036
Wind speed La Perouse Bank	0.015	0.188
Lag 1 week wind speed La Perouse Bank	0.009	0.313
Lag 2 weeks wind speed La Perouse Bank	0.005	0.457
Lag 3 weeks wind speed La Perouse Bank	0.018	0.146
Lag 52 weeks wind speed	0.005	0.445
Upwelling 48°N	0.004	0.514
Lag 1 week upwelling 48°N	0.000	1.000
Lag 2 weeks upwelling 48°N	0.001	0.697
Lag 3 weeks upwelling 48°N	0.001	0.682
Lag 52 weeks upwelling 48°N	0.013	0.219
Upwelling 51°N	0.007	0.350
Lag 1 week upwelling 51°N	0.003	0.527
Lag 2 weeks upwelling 51°N	0.005	0.445
Lag 3 weeks upwelling 51°N	0.003	0.556
Lag 52 weeks upwelling 51°N	0.000	0.918
Sunlight Tofino	0.017	0.311
Lag 1 week sunlight Tofino	0.001	0.847
Lag 2 weeks sunlight Tofino	0.001	0.832
Lag 3 weeks sunlight Tofino	0.005	0.581
Lag 52 weeks sunlight Tofino	0.002	0.747
Lag 1 week whales per survey	0.630	0.000

Lag 2 weeks whales per survey	0.428	0.000
Lag 3 weeks whales per survey	0.203	0.000
Lag 52 weeks whales per survey	0.001	0.818

Table 15. Single regressions – week: environmental variables. Variables explaining ≥10% of the variance and with a p-value of ≤0.1 are highlighted in grey. Independent variables are listed in the 'Variables' column; the R^2 column represents the R^2 value of the regression and the 'p' column lists the significance of each regression.

Variable	**R^2**	**Sig.**
Year	0.002	0.614
Week	0.000	0.924
Week = 1	-	-
Week = 2	-	-
Week = 3	-	-
Week = 4	-	-
Week = 5	-	-
Week = 6	-	-
Week = 7	-	-
Week = 8	-	-
Week = 9	-	-
Week = 10	-	-
Week = 11	-	-
Week = 12	-	-
Week = 13	-	-
Week = 14	-	-
Week = 15	-	-
Week = 16	-	-
Week = 17	-	-
Week = 18	-	-
Week = 19	-	-
Week = 20	-	-
Week = 21	-	-
Week = 22	-	-
Week = 23	-	-
Week = 24	-	-
Week = 25	-	-
Week = 26	-	-
Week = 27	-	-
Week = 28	-	-
Week = 29	-	-
Week = 30	-	-
Week = 31	-	-
Week = 32	-	-
Week = 33	-	-

Week = 34	-	-
Week = 35	-	-
Week = 36	-	-
Week = 37	-	-
Week = 38	-	-
Week = 39	-	-
Week = 40	-	-
Week = 41	-	-
Week = 43	-	-
Week = 43	-	-
Week = 44	-	-
Week = 45	-	-
Week = 46	-	-
Week = 47	-	-
Week = 48	-	-
Week = 49	-	-
Week = 50	-	-
Week = 51	-	-
Week = 52	-	-

Table 16. Single regressions – week: temporal variables. Variables explaining ≥10% of the variance and with a p-value of ≤0.1 are highlighted in grey. Independent variables are listed in the 'Variables' column; the R^2 column represents the R^2 value of the regression and the 'p' column lists the significance of each regression.

Variable	**R^2**	**Sig.**
Semi-month period	0.003	0.660
Lag 1 period whales per survey	0.512	0.000
Lag 2 periods whales per survey	0.075	0.059
Lag 3 periods whales per survey	0.004	0.692
Lag 26 periods whales per survey	0.007	0.549
SST Amphitrite	0.118	0.006
Lag 1 period SST Amphitrite	0.052	0.071
Lag 2 periods SST Amphitrite	0.034	0.147
Lag 3 periods SST Amphitrite	0.022	0.245
Lag 26 periods SST Amphitrite	0.035	0.138
SST Nootka	0.161	0.001
Lag 1 period SST Nootka	0.089	0.016
Lag 2 periods SST Nootka	0.078	0.026
Lag 3 periods SST Nootka	0.048	0.083
Lag 26 periods SST Nootka	0.034	0.142
Salinity Amphitrite	0.019	0.282
Lag 1 period salinity Amphitrite	0.053	0.068
Lag 2 periods salinity Amphitrite	0.081	0.023
Lag 3 periods salinity Amphitrite	0.042	0.103

Lag 26 periods salinity Amphitrite	0.023	0.227
Salinity Nootka	0.072	0.032
Lag 1 period salinity Nootka	0.034	0.146
Lag 2 periods salinity Nootka	0.023	0.236
Lag 3 periods salinity Nootka	0.041	0.108
Lag 26 periods salinity Nootka	0.088	0.018
Wind speed La Perouse Bank	0.030	0.170
Lag 1 period wind speed La Perouse Bank	0.018	0.289
Lag 2 periods wind speed La Perouse Bank	0.055	0.062
Lag 3 periods wind speed La Perouse Bank	0.104	0.009
Lag 26 periods wind speed La Perouse Bank	0.000	0.874
Upwelling 48°N	0.013	0.361
Lag 1 period upwelling 48°N	0.004	0.604
Lag 2 periods upwelling 48°N	0.003	0.669
Lag 3 periods upwelling 48°N	0.004	0.642
Lag 26 periods upwelling 48°N	0.021	0.258
Upwelling 51°N	0.015	0.333
Lag 1 period upwelling 51°N	0.016	0.316
Lag 2 periods upwelling 51°N	0.018	0.297
Lag 3 periods upwelling 51°N	0.022	0.241
Lag 26 periods upwelling 51°N	0.001	0.763
Sunlight Tofino	0.053	0.196
Lag 1 period sunlight Tofino	0.001	0.863
Lag 2 periods sunlight Tofino	0.012	0.552
Lag 3 periods sunlight Tofino	0.007	0.671
Lag 26 periods sunlight Tofino	0.008	0.685

Table 17. Single regressions – semi-month: environmental variables. Variables explaining ≥10% of the variance and with a p-value of ≤0.1 are highlighted in grey. Independent variables are listed in the 'Variables' column; the R^2 column represents the R^2 value of the regression and the 'p' column lists the significance of each regression.

Variable	**R^2**	**Sig.**
Year	0.003	0.650
Year = 1997	0.004	0.642
Year = 1998	0.065	0.042
Year = 1999	0.005	0.252
Year = 2000	0.079	0.024
Year = 2001	0.086	0.018
Year = 2002	0.103	0.010
Year = 2003	0.004	0.607
Year = 2004	0.029	0.178
Period = 1	-	-
Period = 2	-	-
Period = 3	-	-

Period = 4	-	-
Period = 5	-	-
Period = 6	-	-
Period = 7	-	-
Period = 8	-	-
Period = 9	-	-
Period = 10	0.001	0.830
Period = 11	0.042	0.106
Period = 12	0.022	0.241
Period = 13	0.001	0.824
Period = 14	0.067	0.039
Period = 15	0.067	0.039
Period = 16	0.002	0.698
Period = 17	0.001	0.816
Period = 18	0.020	0.263
Period = 19	0.005	0.579
Period = 20	-	-
Period = 21	-	-
Period = 22	-	-
Period = 23	-	-
Period = 24	-	-
Period = 25	-	-
Period = 26	-	-

Table 18. Single regressions – semi-month: temporal variables. Variables explaining ≥10% of the variance and with a p-value of ≤0.1 are highlighted in grey. Independent variables are listed in the 'Variables' column; the R^2 column represents the R^2 value of the regression and the 'p' column lists the significance of each regression.

Variable	**R^2**	**Sig.**
SST Amphitrite	0.147	0.021
Lag 1 month SST Amphitrite	0.037	0.260
Lag 2 months SST Amphitrite	0.015	0.483
Lag 3 months SST Amphitrite	0.014	0.493
Lag 12 months SST Amphitrite	0.071	0.117
SST Nootka	0.197	0.007
Lag 1 month SST Nootka	0.061	0.146
Lag 2 months SST Nootka	0.013	0.508
Lag 3 months SST Nootka	0.001	0.853
Lag 12 months SST Nootka	0.079	0.097
Salinity Amphitrite	0.002	0.780
Lag 1 month salinity Amphitrite	0.063	0.715
Lag 2 months salinity Amphitrite	0.000	0.990
Lag 3 months salinity Amphitrite	0.006	0.645
Lag 12 months salinity Amphitrite	0.015	0.471

Salinity Nootka	0.100	0.061
Lag 1 month salinity Nootka	0.033	0.287
Lag 2 months salinity Nootka	0.028	0.329
Lag 3 months salinity Nootka	0.004	0.715
Lag 12 months salinity Nootka	0.026	0.347
Wind speed La Perouse Bank	0.023	0.380
Lag 1 month wind speed La Perouse Bank	0.070	0.119
Lag 2 months wind speed La Perouse Bank	0.141	0.024
Lag 3 months wind speed La Perouse Bank	0.035	0.276
Lag 12 months wind speed La Perouse Bank	0.000	0.972
Upwelling 48°N	0.059	0.153
Lag 1 month upwelling 48°N	0.026	0.347
Lag 2 months upwelling 48°N	0.021	0.397
Lag 3 months upwelling 48°N	0.016	0.469
Lag 12 months upwelling 48°N	0.036	0.269
Upwelling 51°N	0.059	0.152
Lag 1 month upwelling 51°N	0.069	0.121
Lag 2 months upwelling 51°N	0.053	0.178
Lag 3 months upwelling 51°N	0.029	0.321
Lag 12 months upwelling 51°N	0.004	0.714
Sunlight Tofino	0.118	0.041
Lag 1 month sunlight Tofino	0.040	0.244
Lag 2 months sunlight Tofino	0.008	0.599
Lag 3 months sunlight Tofino	0.017	0.442
Lag 12 months sunlight Tofino	0.104	0.055
Lag 1 month whales per survey	0.105	0.092
Lag 2 months whales per survey	0.026	0.499
Lag 3 months whales per survey	0.012	0.740
Lag 12 months whales per survey	0.025	0.399

Table 19. Single regressions – month: environmental variables. Variables explaining ≥10% of the variance and with a p-value of ≤0.1 are highlighted in grey. Independent variables are listed in the 'Variables' column; the R^2 column represents the R^2 value of the regression and the 'p' column lists the significance of each regression.

Variable	**R^2**	**Sig.**
Year	0.000	0.947
Month = January	-	-
Month = February	-	-
Month = March	-	-
Month = April	-	-
Month = May	0.034	0.285
Month = June	0.000	0.906
Month = July	0.166	0.014
Month = August	0.014	0.499

Month = September	0.030	0.313
Month = October	-	-
Month = November	-	-
Month = December	-	-
Year = 1997	-	-
Year = 1998	-	-
Year = 1999	-	-
Year = 2000	-	-
Year = 2001	-	-
Year = 2002	-	-
Year = 2003	-	-
Year = 2004	-	-

Table 20. Single regressions – month: temporal variables. Variables explaining ≥10% of the variance and with a p-value of ≤0.1 are highlighted in grey. Independent variables are listed in the 'Variables' column; the R^2 column represents the R^2 value of the regression and the 'p' column lists the significance of each regression.

Variable	**R^2**	**Sig.**
SST Amphitrite	0.243	0.214
Lag 1 year SST Amphitrite	0.074	0.515
Lag 2 years SST Amphitrite	0.062	0.553
SST Nootka	0.351	0.122
Lag 1 year SST Nootka	0.083	0.488
Lag 2 years SST Nootka	0.005	0.870
Salinity Amphitrite	0.040	0.635
Lag 1 year salinity Amphitrite	0.077	0.506
Lag 2 years salinity Amphitrite	0.011	0.805
Salinity Nootka	0.126	0.389
Lag 1 year salinity Nootka	0.037	0.647
Lag 2 years salinity Nootka	0.366	0.112
Wind speed La Perouse	0.646	0.016
Lag 1 year wind speed La Perouse Bank	0.064	0.546
Lag 2 years wind speed La Perouse Bank	0.064	0.546
Upwelling 48°N	0.082	0.491
Lag 1 year upwelling 48°N	0.013	0.790
Lag 2 years upwelling 48°N	0.457	0.066
Sunlight Tofino	0.153	0.338
Lag 1 year sunlight Tofino	0.126	0.389
Lag 2 year sunlight Tofino	0.202	0.264
Lag 1 whales per survey	0.014	0.800
Lag 2 whales per survey	0.022	0.780
Upwelling 42°N	0.227	0.233
Lag 1 year upwelling 42°N	0.060	0.558
Lag 2 upwelling 42°N	0.037	0.647

Upwelling 45°N	0.003	0.892
Lag 1 year upwelling 45°N	0.045	0.613
Lag 2 years upwelling 45°N	0.552	0.035
Upwelling 54°N	0.633	0.018
Lag 1 year upwelling 54°N	0.047	0.479
Lag 2 years upwelling 54°N	0.222	0.238
Lag 1 year whales per survey	0.014	0.800
Lag 2 years whales per survey	0.022	0.780

Table 21. Single regressions – year: environmental variables. Variables explaining ≥10% of the variance and with a p-value of ≤0.1 are highlighted in grey. Independent variables are listed in the 'Variables' column; the R^2 column represents the R^2 value of the regression and the 'p' column lists the significance of each regression.

Variable	**R^2**	**Sig.**
Year	0.010	0.818
1997	0.004	0.877
1998	0.178	0.297
1999	0.082	0.491
2000	0.220	0.241
2001	0.219	0.243
2002	0.344	0.126
2003	0.017	0.757
2004	0.078	0.502

Table 22. Single regressions – year: temporal variables. Variables explaining ≥10% of the variance and with a p-value of ≤0.1 are highlighted in grey. Independent variables are listed in the 'Variables' column; the R^2 column represents the R^2 value of the regression and the 'p' column lists the significance of each regression.

Year removed	R^2	Sig.	R^2	Sig.	R^2	Sig.
	Wind speed LPB	Wind speed LPB	Lag 2 years upwelling 48N	Lag 2 years upwelling 48N	Wind speed LPB, Lag 2 years upwelling 48N	Wind speed LPB, Lag 2 years upwelling 48N
none	0.646	0.016	0.457	0.066	0.896	0.004
1997	0.645	0.030	0.624	0.061	0.966	0.006
1998	0.760	0.010	0.394	0.182	0.871	0.046
1999	0.673	0.024	0.411	0.170	0.892	0.035
2000	0.604	0.069	0.355	0.289	0.908	0.092
2001	0.723	0.015	0.327	0.236	0.897	0.033
2002	0.486	0.082	0.569	0.083	0.842	0.063
2003	0.639	0.031	0.453	0.089	0.895	0.011
2004	0.648	0.029	0.465	0.091	0.911	0.008

Table 23. Change in R^2 and significance values of single regressions of wind speed and upwelling against whales per survey as observations are removed.