

**Shifts in North Pacific ecosystems and their relationships to regional
climate variability**

**Submitted by Sarah Jane King to the University of Exeter
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Abstract

This study examines how the marine ecosystem along the western coast of North America has been affected by the pattern of the Pacific Decadal Oscillation (PDO) index and sea surface temperatures between 1950 and 2012. Previous studies on this topic have largely failed to incorporate the role of seabirds in the Pacific ecosystem. Data of commercial fish catch and seabird sightings were used for seven fish species and three bird species in California, Oregon, Washington and Alaska, as well as zooplankton biomass in California. Statistical tests were used to examine whether population sizes of these species changed in response to the potential phase shifts of the PDO index in 1977 and 1989. The results of this study indicate that the 1977 phase shift in the PDO index was actually a transition period from a 'cool' to a 'warm' phase that lasted approximately ten years from 1972 until the mid-1980s. This change was associated with marine ecosystem responses at all trophic levels. There is also some evidence for the presence of a second PDO phase change in 1989 and an associated ecosystem response. However, ecosystem changes at this time were less pronounced than those in the 1970s, probably because the PDO index was out of phase with ENSO variability. Responses of marine species to phase shifts in the PDO index were not synchronous across all U.S. states, with a particularly strong latitudinal pattern emerging for species of Pacific salmon. Furthermore, the results presented here indicate that localised sea surface temperature (SST) anomalies with the long-term global warming signal removed, may be able to account for more variation in population sizes than the PDO index, on the western coast of North America. These findings are important because they further our understanding of how species population sizes are affected by regional climate variability and they have the potential to inform decision making for fishing quotas and management plans in the region.

Table of Contents

Definition of Pacific Decadal Oscillation index	5
Hypotheses	5
Aims	5
1. Introduction	7
1.1 Tipping points	7
1.2 Regime shifts	7
1.3 Pacific Decadal Oscillation (PDO)	15
1.4 Impacts on marine ecosystems	18
1.5 Impacts on seabirds	25
1.6 Future change	30
1.7 Relation to previously used methods	31
1.8 Likely impact of research	32
2. Data sources and methods	33
2.1 Commercial fisheries	33
2.2 Macrozooplankton biomass	34
2.3 Seabird abundance	35
2.4 Climate indices	35
2.5 Statistical analysis	36
3. Results	39
3.1 Tests for significant differences in medians of bird and fish populations between PDO phases	43
3.2 Mann-Kendall tests for significant trends	50
3.3 Linear models	56
4. Discussion	60
4.1 Interpretation of main results	60
4.2 Limitations	76
5. Conclusion	79
Appendix 1: R codes	81
Bibliography	92

List of figures and tables

Figure 1. Map of the East Pacific region, showing US states of Alaska (AK), Washington (WA), Oregon (OR) and California (CA)	6
Figure 2. Illustration of the difference between white and red noise	9
Equation 1. AR(1) model	10
Figure 3. A schematic diagram of how an ecosystem displaying regime shifts may switch between alternative stable states	11
Figure 4. Double-integration hypothesis, showing the two stages of integration, with PDO index and zooplankton timeseries as an example	12
Figure 5. The Pacific Decadal Oscillation (PDO) index showing phase shifts in 1925, 1947, 1977 and 1989	16
Figure 6. Stacked area graph showing the contribution of each salmon species to total commercial salmon catch across all states	21
Figure 7. Diagram showing how upwelling occurs along the eastern boundary of the Pacific Ocean	24
Figure 8. Map of the Pacific region showing SST data from the HadISST dataset with black boxes representing (from North to South) the areas of Alaska, Washington, Oregon and California	34
Figure 9. Stacked area graph showing the contribution of each fish species to total commercial catch across all states	39
Figure 10. Stacked area graphs showing the contribution of each bird species to total sightings across all states	41
Figure 11. Graphs of climate indices used in this study annual (a) and winter (b) Pacific Decadal Oscillation index and HadISST data with seasonal cycle removed (c) and warming trend removed (d)	43
Figure 12. Box and whisker plots showing quantities of coho salmon (a), sockeye salmon (b), chum salmon (c), Chinook salmon (d) and pink salmon (e) caught in all states over three time periods	46
Figure 13. Box and whisker plots showing quantities of sardine (a) and herring (b) caught in all states, all fish species in all states combined (c) and zooplankton biomass in California (d) over three time periods	47
Figure 14. Box and whisker plots of common murre (a), marbled murrelet (b), double-crested cormorant (c) and all three species of birds combined (d) over three time periods	50
Table 1. Mann-Kendall test results for climate indices	51
Table 2. Mann-Kendall test results for salmonid fish species in all states and each region separately	53
Table 3. Mann-Kendall test results for non-salmonid fish, all fish species combined and zooplankton	54
Table 4. Mann-Kendall test results for bird species in all states and each region separately	55
Table 5. Linear model results for the five species of Pacific salmon	57
Table 6. Linear model results for non-salmonid marine species	58
Table 7. Linear model results for bird species	59

Definition of the Pacific Decadal Oscillation index

Pacific Decadal Oscillation (PDO) is defined as an index that describes a pattern of regional climatic variability, which is influenced by the Aleutian Low pressure system and characterised by two distinct phases of sea surface temperature (SST) across the North Pacific, a 'warm' (positive) phase and a 'cool' (negative) phase (Mantua and Hare, 2002).

Hypotheses

1. Phase shifts of the Pacific Decadal Oscillation (PDO) index have influenced population sizes of fish and bird species in the Pacific Ocean ecosystem
2. Warm (positive) phases of PDO reduce productivity and population size of local fish and bird species
3. Responses to phase shifts of the PDO index vary between the different trophic levels of zooplankton, fish and bird species in the Pacific Ocean ecosystem
4. Responses of species to PDO phase shifts vary latitudinally from north to south along the western coast of North America
5. Sea surface temperature (SST) data from the HadISST dataset will explain less variation in populations of fish and bird species than the PDO index

Aims

This study aims to investigate how the pattern of forcing from the Pacific Decadal Oscillation (PDO) index has changed over time, from 1950 to 2012 and whether such changes have driven regime shifts in the marine ecosystem. The Pacific ecosystem response to specific PDO phase shifts in 1976 to 1977 and 1989 will be analysed to try to identify how the phases of the PDO index influence population sizes of fish and bird species and whether there are varying reactions between different trophic levels. The investigation will focus on the western coast of the North American continent, as a wealth of information on the Pacific Ocean ecosystem is available from this coastline. To examine spatial and specifically latitudinal effects on the ecosystem in more detail, the coastline is divided into segments from north to south by Pacific U.S. state: Alaska, Washington, Oregon and California (see figure 1).

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Figure 1. Map of the East Pacific region, showing US states of Alaska (AK), Washington (WA), Oregon (OR) and California (CA). (Google maps, 2015)

1. Introduction

1.1 Tipping points

The focus of this study is embedded in the concept of climate tipping elements- the idea that gradual anthropogenic induced warming can trigger Earth systems to reach and exceed critical points, whereby the system is forced by a small perturbation, which causes it to abruptly exhibit fundamentally different properties (Lenton et al., 2008). These tipping points have been suggested in many components of the Earth system, including changes in El-Nino Southern Oscillation (ENSO) amplitude and frequency (Lenton et al., 2008). Similar changes may be occurring in the Pacific Decadal Oscillation (PDO) index, with some evidence suggesting reductions in variance of PDO in recent years (Litzow and Mueter, 2014). The key issue for the research presented here, is the possibility of ecosystem tipping points occurring in the Pacific, whereby marine fish and seabird populations could exceed a threshold causing them to abruptly change, potentially threatening ecosystem services (Scheffer et al., 2009).

1.2 Regime Shifts

A universal definition of a regime shift has yet to be agreed upon in the scientific literature (Litzow and Mueter, 2014). However, they are generally described as changes in modes of low-frequency variability (Litzow et al., 2014). A system exhibiting regime shifts has multiple states that are separated by an unstable equilibrium (Scheffer et al., 2001). Some researchers suggest that these states are stable (Brock and Carpenter, 2010; Overland et al., 2010). However, this is a highly contentious subject, with many researchers disagreeing with the concept of stable states within regime shifts and instead proposing that the regimes are dynamic and they fluctuate around an attractor (Hare and Mantua, 2000; Mollmann et al., 2015; Scheffer and Carpenter, 2003)

1.2.1 In oceans

It is generally accepted that ocean systems are forced by variability of the atmosphere, which is essentially white noise (Hasselmann, 1982). This atmospheric white noise is integrated by the climatic system and converted into higher variance red noise (Hasselmann, 1982). The differences between white

and red noise are illustrated in figure 2. There is no clear evidence for the presence of regime shifts in the oceans and therefore, there is ongoing scientific debate in this area. Physical timeseries from the North Pacific have shown no regime shift behaviour over the last century (Hsieh et al., 2005). Instead, physical variables in the North Pacific Ocean may show behaviours that are linear and stochastic (random) in nature (Hsieh et al., 2005). The main difficulty in determining whether regime shifts occur in the PDO index is the relative shortness of the record (Overland et al., 2006). There is evidence which suggests that composite analysis of multiple short timeseries may find significant regime shifts, when there is actually nothing more than Gaussian red noise and stationary statistics (Rudnick and Davis, 2003). However, researchers have suggested that a conceptual model of regime-like behaviour in North Pacific variability cannot be ruled out (Overland et al., 2006).

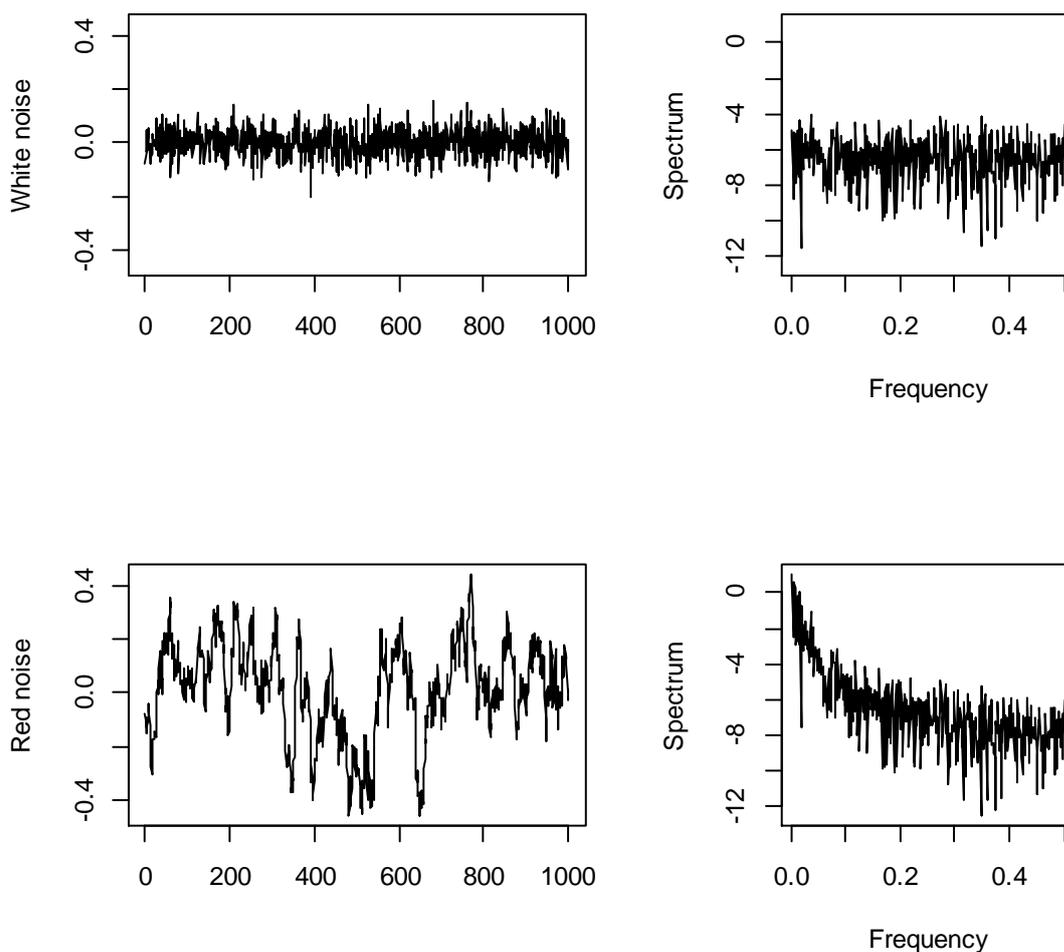


Figure 2. Illustration of the difference between white noise (e.g. atmospheric forcing) and red noise (e.g. PDO climate index) showing the power spectrums, with white noise having almost equal power at all frequencies and red noise having higher power at lower frequencies

Under random walk variability a climate system will exhibit gradual, random change over time with no stable states and has the potential for increasing variance (Hare and Mantua, 2000). Random walk is a red noise process, which occurs when contributions from different frequency signals combine in a random manner (Overland et al., 2010). The red noise process is often expressed as an autoregressive model (AR-1) (see equation 1), where the rate of change of a physical ocean variable is forced by the integration of white noise variations from the atmosphere (Hasselmann, 1982). This model also sometimes includes

the amount of memory in the climate system. The pattern of the PDO index can be explained in this way, as the integration of random weather events, creating variability by chance (Doney and Sailley, 2013).

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Equation 1. AR(1) model where $d\phi(t)/dt$ is the rate of change of the ocean variable, $f(t)$ is white noise variations of the atmosphere and T_{ocean} is the dampening of the signal with natural dissipation time of the ocean variable (Di Lorenzo and Ohman, 2013)

1.2.2 In ecosystems

Ecological regime shifts are a more widely accepted idea than regime shifts in the ocean, but they are still debateable. Changes in the ecosystem of the Pacific Ocean can be explained by two different models. The first of these is that the marine ecosystem does display non-linear regime shifts, whereby the ecosystem has two alternative states, driven by the 'warm' and 'cool' phases of Pacific Decadal Oscillation and separated by an unstable equilibrium (Scheffer et al., 2001). This pattern of shifts between the states can occur in a forwards or backwards direction with different forcing conditions (see figure 3) and is referred to as hysteresis (Scheffer et al., 2001). Shifts between these two stable states often occur suddenly and without any early warning (Scheffer et al., 2001). This is due to resilience in the ecosystem which equates to the size of the basin attraction around a state and can be reduced by gradually changing environmental conditions, until a critical threshold is met and exceeded (Scheffer et al., 2001).

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Figure 3. A schematic diagram of how an ecosystem displaying regime shifts may switch between alternative stable states in a forwards or backwards direction (Scheffer et al., 2001)

The second model that can be used to explain ocean ecosystem responses to climatic forcing is the double-integration hypothesis (see figure 4). This was proposed by Di Lorenzo and Ohman (2013) and involves the double-integration of atmospheric white noise that can separate regime-like behaviours from random noise in ecosystems. It is based on the idea that white noise from the atmosphere, which drives red noise ocean processes, results in redder noise in biological systems (Doney and Salliey, 2013). The integration of this noise can generate marine ecosystem responses that are similar to regime shifts, with prolonged state changes and strong transitions in populations (Di Lorenzo and Ohman, 2013). However, these regime-like phases are not statistically distinct from integrated random noise (Di Lorenzo and Ohman, 2013).

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Figure 4. Double-integration hypothesis, showing the two stages of integration, with PDO index and zooplankton timeseries as an example (adapted from Di Lorenzo & Ohman 2013)

Abrupt shifts in environmental variables such as sea surface temperature (SST) can either be caused by stochastic (random) processes or nonlinear processes (Hsieh et al., 2005). There is some evidence to show that complex marine ecosystems can respond quickly to stochastic fluctuations in environmental variables because they behave in a dynamically nonlinear way (Hsieh et al., 2005). However, it has also been suggested that pelagic fish populations can simply track stochastic environmental variables in a linear way (Hsieh and Ohman, 2006). This study found that populations are most likely to behave linearly when the generation time of the species matches the timescale of the environmental fluctuation (Hsieh and Ohman, 2006). Therefore, there is considerable scientific debate as to whether biological populations respond to changes in environmental variables in a non-linear or in a linear manner.

If ecological regime shifts do occur, they can involve abrupt and often long-lasting changes in ecosystems which may have significant effects on human communities and economics (Biggs et al., 2009), especially when related to impacts on fisheries. In areas largely free from overfishing, climate regime shifts are considered to be the dominant drivers of ecological variability, at decadal timescales (Litzow et al., 2014). However, in areas that are regularly exploited by the fishing industry, overfishing can increase the rapidity and frequency with which regime-like shifts in marine ecosystems occur (Steele, 1998). These sudden changes are often preceded by a perturbation that under previous stable conditions would have had little effect on the ecosystem (Biggs et al., 2009). Such abrupt shifts have been demonstrated in many ecosystems worldwide including lakes, coral reefs, woodlands and deserts, as well as in the oceans (Scheffer et al., 2001). The ecosystem in the Pacific Ocean exhibits these regime-like phases and may be reaching a critical tipping point in the

frequency and amplitude of shifts over time, due to climatic warming and forcing from the Pacific Decadal Oscillation index.

1.2.3. Early Warning

It has been suggested that regime shifts may show early warning signals which could be identified and used to avert potentially catastrophic changes in systems (Contamin and Ellison, 2009). In some circumstances variations in ecological time series could be used as early warning indicators of climatic regime shifts (Biggs et al., 2009). In fact, in the Pacific Ocean cyclical variations in sardine populations were observed before the physical conditions of sea surface temperature (SST) and circulation that comprises the PDO index were fully described (Chavez et al., 2003). In ecological time series, indications that the system is approaching a threshold may include: an increase in variability, changes in skewness and slower population recovery rates from small perturbations (Biggs et al., 2009). Contamin and Ellison (2009) estimate that for an indicator to be effective as an early warning of a change to an ecosystem it needs to identify a shift at least 20 years into the future. This is in order to enable changes in the management of the ecosystem concerned. For example, agricultural inputs into a lake could be controlled to prevent it crossing a threshold and entering a different nutrient regime (Contamin and Ellison, 2009). In the Pacific Ocean, recommended catch levels of many salmon runs are calculated based on data of population sizes before the ecological regime shift in the mid-1970s (Hare and Mantua, 2000). This change in management practices has occurred because it has been recognised that more recent data may not be relevant to modelling present day conditions. Salmon runs could also be managed so that harvest is reduced when there is a suspected impending regime shift and freshwater habitats used for spawning could be restored (Biggs et al., 2009). Provided management practices can be adjusted swiftly, it is estimated that a 20 year warning period would reduce the chance of a major ecological regime shift occurring to less than 5% (Contamin and Ellison, 2009).

In physical climate variables early warning indicators could be looked for in the low frequency bands of variance spectrums (Contamin and Ellison, 2009). However, it can be very difficult to determine either in advance or in real time whether a climate regime shift is 'genuine' or 'false'. For example, in 1958 the

PDO index exhibited a 'false' regime shift with the PDO phase reversing for only two years before switching back (Monastersky, 2000). These false shifts in the system mean that a period of up to 10 years is often needed in hindsight after a transition to identify whether it has persisted and does qualify as a significant change (Monastersky, 2000). In addition, Petersen et al. (2008) caution that most marine data are insufficient to identify discontinuous climatic regime shifts and to provide early warning indicators for them. As such identifying early warning indicators of regime shifts in the Pacific Decadal Oscillation index is beyond the scope of this study.

1.2.4. In the Pacific Ocean

There is some current debate as to whether the pattern of 'warm' and 'cool' phase shifts within the Pacific Ocean is changing over time, how this will influence ecosystems and whether this change represents a tipping element in the Earth system. Litzow and Mueter (2014) found reductions in variance of PDO over the last few decades and they suggest that this might be an indicator of further long term change. There is also evidence suggesting that the PDO index is reddening over time, meaning that there are more quasi-cyclic features in the system (Steele et al., 1994). This study aims to investigate such evidence of changes in the PDO to form a clearer picture of whether these signals are being carried through marine ecosystems and how any changes in the PDO index are manifesting themselves in population sizes of marine species.

1.3 Pacific Decadal Oscillation (PDO)

1.3.1. Calculation and history

The Pacific Decadal Oscillation (PDO) index is calculated as the first principle component (PC) of sea surface temperature (SST) in the Pacific Ocean, north of 20°N and is generally used as a winter index between November and March (Goodrich, 2004). The PDO index is sometimes also referred to as Interdecadal Pacific Oscillation (IPO), but this term includes information on the state of the Pacific Ocean from the southern hemisphere as well as the northern hemisphere (Vance et al., 2015). Therefore, to avoid confusion this term will not be used in this study.

Tree-ring and coral based climate reconstructions indicate that variations in the PDO index can be dated back to at least the 1600s (Mantua and Hare, 2002). Phase shifts in the PDO index develop over decadal scales and have occurred at a frequency of approximately one every 25 to 35 years since at least 1890 (Mantua et al., 1997). However, there is some debate about this as it has been suggested that PDO phases may have two major periodicities of between 15 to 20 and 70 years (Brown et al., 2001), with short-term sign reversals common within these longer periods (Mantua, 2002).

Additionally, the PDO index has proven to be difficult to include in climate models due to the horseshoe pattern of SST anomalies and therefore most models are still unable to accurately capture its influence on global climate (Douville et al., 2015). The simulated pattern of the PDO index in models is also highly dependent on the position of the Aleutian Low pressure system within the model run (Yim et al., 2015), this illustrates how important each model component can be on the overall outcome.

Nevertheless, there are several well documented phase shifts in the Pacific Decadal Oscillation index, there have been two full cycles of negative and positive values between 1890 and the mid-1990s (Mantua, 2002). A cool phase prevailed between 1890 and 1924, with a shift to a warm phase occurring in 1925 and continuing until 1946 (Mantua, 2002). Thereafter, there was another cool phase between 1947 and 1976 with a major shift to a warm phase in 1977 (see figure 5), which possibly persisted into the mid-1990s (Mantua, 2002). The most well studied of these phase changes are unsurprisingly also the most

recent, these occurred in the winter of 1976-1977 and potentially in 1989 (Hare and Mantua, 2000). The phase shift in 1989 is debated, some previous research has indicated that it may not be present in the PDO index, but it does appear in other climate indices (Benson and Trites, 2002). Earlier shifts in the 1920s and the mid-1940s have also been suggested but they have been sparsely studied (Hare and Mantua, 2000) and there is little data on the status of marine populations at this time. Therefore, these earlier regime shifts are not included and instead this study focuses on investigating marine responses to the PDO index phase changes in 1977 and potentially in 1989.

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Figure 5. The Pacific Decadal Oscillation (PDO) index showing phase shifts in 1925, 1947, 1977 and potentially in 1989 (adapted from Hare et al. 1999)

1.3.2. Relation to El-Nino Southern Oscillation

The Pacific Decadal Oscillation is closely related to other modes of climatic variability. In fact, there is some evidence that PDO may not be a mode of variability itself, but instead it may be a low frequency residual of El-Nino Southern Oscillation (ENSO) (Overland et al., 2010). This is contested with Hare and Mantua (2000) identifying two features that distinguish between the PDO index and ENSO. They suggest that PDO and ENSO are separate modes of variability because the PDO index's effect on climate is most visible in the North Pacific with secondary signatures present in the tropics and ENSO's effect on climate is most visible in the tropics, with secondary effects in the North Pacific (Hare and Mantua, 2000). For the purposes of this study, the Pacific Decadal Oscillation index will be considered as an independent mode of climatic variability. Regardless of how it is classified, the PDO index is predicted to remain as a significant mode of environmental variability throughout the 21st Century (Litzow and Mueter, 2014) and as such its potential effects on marine ecosystems are important to understand.

1.3.3. Effects on the Earth System

The Pacific Decadal Oscillation index and sea surface temperature (SST) variability have far-reaching effects across the Pacific Ocean, from the Aleutian Islands to the Southern Pacific, both within the marine system and the atmospheric system. This is because the PDO index has been linked to the altering paths of the jet streams in the area (Brown et al., 2001). Furthermore, fires in the Pacific Northwest region of the USA tend to occur in positive PDO conditions (Hessl et al., 2004) and by exerting influence on spring precipitation across Alaska, the PDO index can determine the extent of lightning-induced fires in the following season (Duffy et al., 2005). These effects across the Pacific Ocean may have been occurring since 1853 with corals in the South China Sea showing a geochemical record of annual PDO activity dating back to this time (Deng et al., 2013).

The Pacific Decadal Oscillation appears to interact with El Niño Southern Oscillation, although this is contentious because, as previously discussed, some researchers think the PDO is a part of ENSO variability. Nevertheless, ENSO appears to be strengthened when it is in-phase with PDO and weakened when it is out of phase (Goodrich, 2004), this interaction causes some interesting phenomena. For instance, the PDO index and ENSO have had a local impact on airborne pollution in North America, with La Niña years that occur concurrently with negative phases of the PDO increasing pollution levels (Kalkstein and Goodrich, 2012). In addition, when the cool phase of the PDO coincides with a cool ENSO period they act together to intensify drought in southwest USA (Woodward et al., 2008). Conversely, there can be benefits to communities when the PDO index and ENSO are out of phase, such as a reduction of the negative effects of El Niño events on crop production in India (Woodward et al., 2008).

However, its impact does not end at the margins of the Pacific Ocean basin, as the PDO has been found to influence other areas of the Earth System. The Aleutian Low pressure system has been found to have an impact on the strength of the PDO index, this interaction can cause shifts in the mid-latitude cyclone track to the south during the warm phase of the PDO and to the north during the cool phase of the PDO (Goodrich, 2004). Furthermore, the PDO index is believed to have an impact on hurricane count in the Atlantic (Varotsos

et al., 2015). It has been found that negative phases of the PDO index generate a warm anomaly over Central Asia which contributes to the onset of the monsoon (Watanabe and Yamazaki, 2014). In addition, differences between the cold and warm phases of the PDO index influence the thermodynamic equilibrium of the South Atlantic Ocean (Soares et al., 2014). Changes in regional sea level in the Pacific Ocean have been linked to the pattern of PDO phases with the PDO index explaining up to 40% of observed sea level rise over the last twenty years (Zongshang and Yongsheng, 2014). Furthermore, recent evidence has linked persistent cool conditions in the eastern tropical Pacific with the global warming hiatus we have experienced of late (Maher et al., 2014) and the PDO index is likely to have had an influence on this (Douville et al., 2015). However, there is also evidence that leads to the conclusion that strengthening of the trade winds since the 1990s (Thompson et al., 2015) and sea surface temperatures in the tropical Pacific have contributed to the lack of increase in observed global mean surface temperature in the last 15 years (Douville et al., 2015).

1.4 Impacts on marine ecosystems

It is perhaps important to note that regime shifts do not necessarily degrade the ecological viability of the marine ecosystem, in many cases the community that emerges from the shift is as diverse as the one that came before it (Steele 1998). However, due to changes in species compositions it may not be as economically valuable to the fishing industry as the previous ecological regime (Steele, 1998). In addition, fishing itself has a vast impact on marine ecosystems across the world and the fishing industry acts very differently to environmental pressures. There is a phenomena that has been referred to as 'fishing down the food web' whereby the larger individuals that are usually at higher trophic levels are selectively removed from the marine ecosystem, thus decreasing the trophic level of populations and unbalancing the food web (Neira et al., 2009). This process can make marine ecosystems more susceptible to sudden, potentially catastrophic changes.

1.4.1. In the Pacific Ocean

The aquatic species that will be investigated as part of this study include all five species of salmon present in the Pacific Ocean, sardine (*Clupeidae spp.*), Pacific herring (*Clupea pallasii*) and macrozooplankton, with more information about each given below. In order to spatially constrain these records it is assumed that all fish landed in a state were caught within the Exclusive Economic Zone, which is within 200 nautical miles or 370km of the shoreline of that state (United Nations, 2013).

In addition to the marine species researched in this study the Pacific Decadal Oscillation index has had further impacts on the Pacific Ocean ecosystem, particularly on predators. The PDO phase change in 1977 has been linked to a large-scale decline in apex predators in the Aleutian Islands; species such as Stellar sea lions and sharks saw decreases in population sizes, which also impacted their prey of pollock and mackerel (Heymans et al., 2007). Cetaceans are particularly affected when the California Current is weakened during the positive phase of PDO, with some species of porpoise and dolphin pushed closer to the shore due to the associated decrease in upwelling and primary productivity effecting their food supply (Heymans et al., 2007).

1.4.2. Salmon (*Oncorhynchus spp.*)

The Pacific Decadal Oscillation (PDO) index has been shown to have significant effects on populations of specific fish species. Species that are especially affected by the PDO are Pacific salmon (genus *Oncorhynchus*). There are six species of salmon in the Pacific Ocean, five of which are present and commercially harvested off the western coast of North America (Eggers et al., 2005) and will therefore be included in this study. These five species are Chinook salmon (*Oncorhynchus tshawytscha*), chum salmon (*Oncorhynchus keta*), coho salmon (*Oncorhynchus kisutch*), pink salmon (*Oncorhynchus gorbuscha*) and sockeye salmon (*Oncorhynchus nerka*). Abundance of each species varies greatly with latitude; pink and sockeye salmon are the most abundant species in Canada (Geiger et al., 2002) and in Alaska (Hare et al., 1999), whereas in Washington, Oregon and California Chinook and coho salmon are the most abundant species (Eggers et al., 2005). All of these species are anadromous (migratory), travelling from oceanic foraging grounds

throughout the Pacific Ocean to their own natal freshwater river to spawn in gravel beds (Dittman and Quinn, 1996). The amount of time taken for juveniles to migrate into the Pacific Ocean is dependent on the species, with pink and chum salmon migrating to sea soon after emergence, whereas sockeye, coho and Chinook salmon rear as juveniles in freshwater for extended periods of time (Eggers et al., 2005). The homing mechanism they use to return to the same river they were spawned in has long been debated with some suggesting they learn the odour of their natal stream and navigate by olfactory (Dittman and Quinn, 1996), while others hypothesised they may use the sun as a celestial compass or navigate using temperature and salinity gradients (Bracis, 2010). However, more recently it has been suggested that Pacific salmon can respond to magnetic field intensity and inclination in order to navigate at sea (Putman et al., 2014).

There are also large differences in the diet of these five species of Pacific salmon. Sockeye, chum and pink salmon are plankton feeders, whereas coho and Chinook salmon feed on actively swimming organisms (Drinkwater et al., 2010). This difference means that at different locations intraspecific variation (variation between individuals of the same species) can often be higher than interspecific variation (variation between individuals of different species) at a specific location (Drinkwater et al., 2010). This is largely due to the fact that plankton feeders (sockeye, pink and chum salmon) show high plasticity in their diet and such switches are often associated with a change in environmental conditions (Drinkwater et al., 2010).

Changing patterns in Pacific salmon abundance have been observed in relation to the modes of the PDO index, especially in the aftermath of the phase shift of 1976-1977 (see figure 6). For example, before the shift Chinook salmon productivity was high and after the shift there was a sharp decline in populations (Levin, 2003). This pattern is difficult to discern in figure 6 because Chinook salmon are not as abundant as other species, but what is apparent is the sharp increase in sockeye and pink salmon stocks in the North Pacific preceding, during and following 1977. It is important to note that there were changes in the numbers of fishing vessels and the fishing equipment used over this period. For example, it is estimated that between 1965 and 1995 technological advancements increased the efficiency of a thirteen meter trawler by an

average of 260% (Sissenwine and Symes, 2007). However, the number of fishing vessels have generally decreased as efficiency has improved (Sissenwine and Symes, 2007). There is therefore little evidence to suggest that the rapid increase of landings of sockeye and pink salmon in the mid-1970s (seen in figure 6) is a direct result of changes in fishing practices.

Throughout the available record Pacific salmon have displayed decadal-scale cycles in abundance with a periodicity of between 25 to 68 years in rivers in British Columbia, Canada and Oregon, North America (Drake and Naiman, 2007). In particular, Northeastern Pacific salmon stocks are heavily affected by the phase of the PDO index, during the positive phase they attain relatively high population sizes and during the negative phase of the PDO stocks are depleted (Drake et al., 2002). This pattern is highly spatial as the opposite is seen in Pacific salmon populations further south along the coastline (Drake et al., 2002).

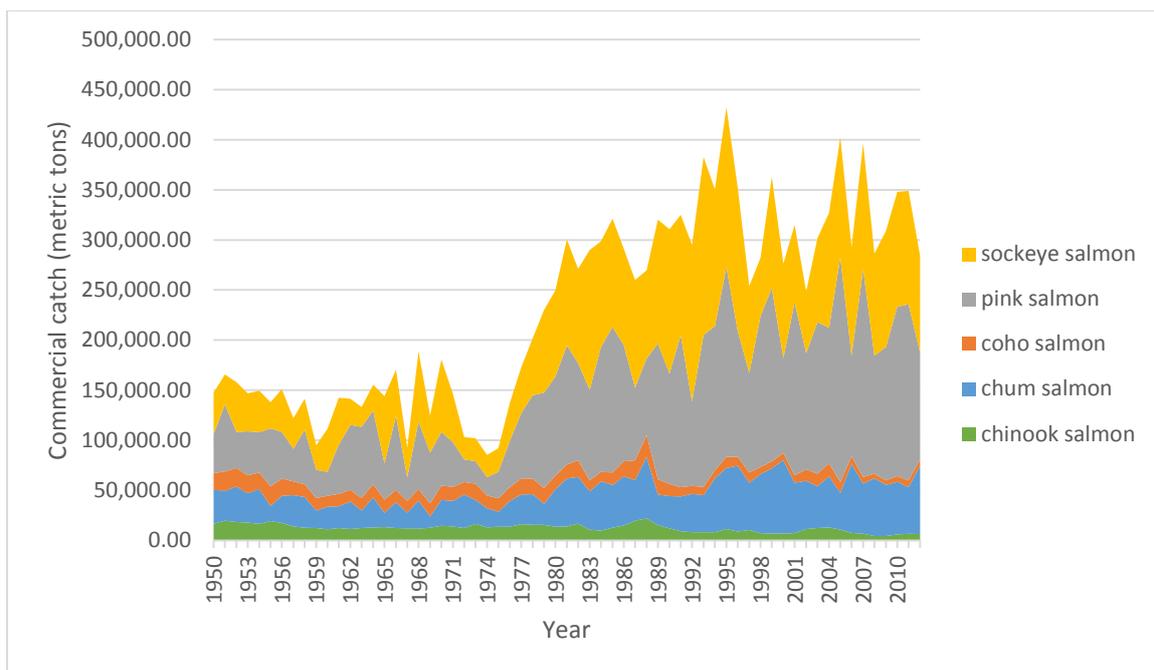


Figure 6. Stacked area graph showing the contribution of each salmon species (in metric tons) used in this study to total commercial salmon catch across all states

1.4.3. Sardine (*Clupeidae spp.*) and Northern anchovy (*Engraulis mordax*)

Observations of sardine populations first identified sea surface temperature (SST) variations in the Pacific (Chavez et al., 2003), which lead to the description and the coining of the term Pacific Decadal Oscillation in 1996 (Mantua, 2002). The warm and cool phases of the PDO index have also been referred to as the sardine and anchovy phases respectively, due to the increase in the relative abundance of these species during each phase of the PDO (Chavez et al., 2003). Abundance of these species is therefore important to monitor as they can be seen as key indicators of regime shifts in the North Pacific. For example, before the phase shift in 1976 cool, anchovy favourable conditions prevailed and after the transition a warmer, sardine regime was dominant (Chavez et al., 2003). However, the abundance of fish species is not just purely effected by climatic regimes, direct effects of fishing practices can dramatically alter the size of certain fish populations that are economically desirable. For instance, sardines were overfished in the California Current off the west coast of North America and in the 1930s the industry collapsed (Tomczak and Godfrey, 1994).

1.4.4. Pacific herring (*Clupea pallasii*)

While the coastal upwelling region along the coast of California, Oregon and Washington supports populations of pelagic species such as sardines and anchovies, the associated downwelling area of the Gulf of Alaska is dominated by benthic or groundfish such as Pacific herring (*Clupea pallasii*) (Francis et al., 1998). There have been relatively few studies examining this species relationship to the Pacific Decadal Oscillation index. In 2008 Deriso et al. found that the most significant factors in the lack of recovery of Pacific herring populations in Prince William Sound, Alaska were competition or predation from juvenile hatchery pink salmon. This study found no statistical correlation between lack of recovery of populations and the PDO index (Deriso et al., 2008). However, they did not examine whether Pacific Decadal Oscillation fluctuations could explain overall population trends of Pacific herring, which is something this study aims to further investigate.

1.4.5. Plankton and chlorophyll

The word plankton is derived from Greek meaning 'that which is made to wander or drift' (King, 1965). There are two broad types of plankton that exist at the base of marine food webs, phytoplankton are photosynthetic organisms and zooplankton are predominantly herbivorous organisms that feed mainly on phytoplankton, both are carried by oceanic currents and their distribution across the Pacific reflects this (Steele, 1977). Therefore, the spatial extent of phytoplankton blooms is highly non-uniform and difficult to predict (Steele, 1977). A key difference between phytoplankton and zooplankton is the ability of some zooplankton species to leave the upper layer of the ocean and perform a diurnal migration to deeper layers during the day, in order to graze phytoplankton more efficiently (Steele, 1977). However, some species of phytoplankton, for example dinoflagellates, also display motility (Yamazaki and Kamykowski, 1991).

Both zooplankton and phytoplankton show hugely regional responses along the Pacific west coast of North America to warming temperatures and to the influence of the Pacific Decadal Oscillation index. In the California Current there is evidence to show that biomass of macrozooplankton (those zooplankton visible to the naked eye) has decreased by as much as 80% between 1951 and 1993, with the ocean surface layer warming by up to 1.5°C in the same period (Roemmich and McGowan, 1995). A recent study has also found that increasing water temperatures are linked to a decrease in the cell size of phytoplankton and an associated reduction in productivity (Gu enette et al., 2014). This is supported by a study into zooplankton community structure that found a latitudinal pattern with temperature gradients, whereby larger species of zooplankton were found in cooler waters, at higher latitudes (Chiba et al., 2015).

During the PDO phase change event of 1976/1977 there were significant changes in phytoplankton abundance near Hawaii as a response to deepening of the mixed layer (Francis et al., 1998). During the warm phase of the PDO after the 1977 shift zooplankton biomass declined off the coasts of Oregon and Washington but increased in Alaska (Chavez et al., 2003). However, another study based in Oregon concluded that phytoplankton abundance has a weak relationship with the PDO index in this region (Menge et al., 2009).

1.4.6. Productivity and upwelling

The abundance of zooplankton and phytoplankton (or primary productivity) has a very close relationship to currents and upwelling systems in the Pacific Ocean. The area of peak primary productivity in the North Pacific is the western coast of North America, with the highest levels of plankton abundance along that coastline at high latitudes in Alaska (Townsend, 2012). Upwelling is defined as the vertical fluctuation of ocean water from below the thermocline into the surface layers, it is strongest along the coast where winds blowing parallel to the coastline drive the offshore transport of surface waters (see figure 7) (García-Reyes et al., 2014). The California Current is an eastern boundary upwelling zone with upwelling in spring and summer reducing sea surface temperatures (SST) to approximately 15°C (Tomczak and Godfrey, 1994). Such upwelling introduces deep nutrient-rich waters to the surface layer and stimulates plankton growth, with upwelling zones comprising 1% of the oceans by area and contributing to 11% of total global primary productivity (Hirata et al., 2009).

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Figure 7. Diagram showing how upwelling occurs along the eastern boundary of the Pacific Ocean (NASA, 2015)

Upwelling along the Pacific coastline of North America is also influenced by the Pacific Decadal Oscillation index. The California Current is particularly susceptible to variations in the PDO index as it changes seasonally; a positive phase of the PDO suppresses coastal upwelling and therefore results in reduced plankton productivity (Barron and Anderson, 2010). This phenomenon occurred after the 1977 shift to a 'warm' or positive phase of PDO as the California Current freshened and became more stratified with upwelling being less effective (Checkley and Barth, 2009). The opposite effect occurs during the negative or 'cool' phase of the PDO index, resulting in increased primary

productivity in California (Barron and Anderson, 2010), this pattern is reversed in the Gulf of Alaska.

1.4.7. Temporal responses

Not all species within the Pacific Ocean ecosystem respond equally to the same environmental forcing. A study by Di Lorenzo and Ohman (2013) showed that different species of zooplankton had contrasting temporal responses, with one species displaying interannual variability explained by atmospheric white noise and another species exhibiting decadal fluctuations. One of the aims of this study is to investigate whether similar differences in responses are found at higher trophic levels among fish species and whether there is any time lag between each species response to a change in environmental conditions. Time lags between responses of species to changes in environmental conditions may be expected since the biological timescale is usually longer than that of the physical ocean (Doney and Sailley, 2013). The exception to this is phytoplankton which has a generation time of approximately one day, meaning it has a close relationship with the response of the upper ocean (Steele, 1977). Time lags are also expected between the responses of marine species, because different species have contrasting generation times and life histories (Hsieh and Ohman, 2006).

1.5 Impacts on seabirds

Seabird populations in the Pacific Ocean basin are in a constant state of flux and are influenced by a number of factors both within the ecosystem and from external environmental conditions. In particular, populations of some species of seabirds have shown fluctuations that are likely related to ENSO (El Niño Southern Oscillation) and PDO (Pacific Decadal Oscillation) conditions across the Pacific Ocean. Following the strong ENSO event in 1982-1983 populations of great frigatebirds and red-footed boobies decreased by as much as 35% in Honolulu, Hawaii and recovery from this event took as long as a decade (Vandenbosch, 2000). Similar responses may occur in some species during the warm phase of the PDO as populations can be suppressed due to the warmer temperatures along the west coast of North America (Vandenbosch, 2000). Therefore, the slow recovery time after the 1983 population declines may be linked to this strong ENSO event being accompanied by a warm phase of the

PDO which further suppressed seabird numbers (Vandenbosch, 2000). A decrease in seabird population sizes in Honolulu, Hawaii was also found following the 1977 PDO reversal (Vandenbosch, 2000). This study aims to replicate these results and investigate the effects of reversals in the PDO index on seabird populations in western North America, using data from the Christmas Bird Count (CBC). Seabirds can be used as indicators of fish populations and environmental conditions if the life history of the species and the population is well known (Parrish and Zador, 2003). Based on this and the data available from the CBC studies three species of seabirds with the most complete records from Alaska, Washington, Oregon and California were chosen, these were: common murre, marbled murrelet and double-crested cormorant.

1.5.1. Common murre (*Uria aalge*)

The life history of the common murre is well known and documented and they are widespread throughout the year along the western coast of North America. Together with the completeness of the Christmas Bird Count (CBC) record this makes it an ideal seabird to include in this study.

Common murres nest on ledges in cliff faces in small groups of tens to hundreds of individuals (Parrish and Zador, 2003), they were the most abundant breeding seabird in 1996 in coastal waters from central California north to Oregon (Ainley et al., 1996). However, their breeding distribution is fragmented with hundreds of thousands of individuals in colonies in Oregon and California and more than a million common murres in colonies in the Gulf of Alaska, but few birds breed on the coasts of Washington and British Columbia, Canada (Hipfner, 2005). During the breeding season they do not stray far from their colonies to forage, usually less than 7km offshore (Matthews, 1983). However the Christmas Bird Count (CBC) is conducted over winter when they have a much greater foraging range of up to 60km offshore (Matthews, 1983).

Common murres are opportunistic foragers, being coastal divers in the breeding season and pelagic divers for the rest of the year (De Graaf et al., 1985). As such, their diet varies depending on location, season and abundance of different fish species (Ainley et al., 1996), and it includes species such as rockfish, anchovy, North Pacific hake, Pacific herring and juvenile salmon

(Matthews, 1983). They also use zooplankton or krill as an important food source during egg formation from April to May, this trophic level switching is similar to their ability to prey switch in that it provides an additional mechanism with which to survive through periods of limited and uncertain prey stocks (Sydeman et al., 1997). However, there is some concern that their ability to switch prey may be under threat from increased pressures of fisheries activities and changing environmental conditions. As such, selection and ingestion of poorer quality food sources, for example surfperch and butterfish may indicate that common murres are under food stress in the region (Ainley et al., 1996).

Whilst environmental conditions such as PDO index reversals may play a role in explaining changing populations of seabirds, there are many additional factors such as human activities, competition and predation within the North American ecosystem that complicate this picture. Since common murres are opportunistic foragers and are widespread along the coastline they have many complex relationships with other species in the region. For example, bald eagles (*Haliaeetus leucocephalus*) may be responsible for a decline of about 3% per year in common murre populations on the Washington coast between 1999 and 2001 (Parrish et al., 2001). This decline was likely caused by bald eagles both directly predating adult murres and indirectly enabling gulls and crows access to the murres eggs (Parrish et al., 2001). Whereas, another study also in Washington gave a convincing report of how a different apex predator-peregrine falcons have increased numbers of common murres in the area. Paine et al. (1990) showed that peregrine falcons predate crows, which in turn reduces common murre egg predation.

Anthropogenic activities have an equally strong influence over common murre populations in North America, as they are one of the most frequently caught species of bycatch in commercial fishery nets (Hipfner, 2005). In the summer of 1968 a high mortality of common murres in north California was correlated with high concentrations of the pesticide DDE which may have contributed to this mortality during a time of environmental stress (Scott et al., 1975). More recently, the 1989 Exxon Valdez oil spill in the Gulf of Alaska was estimated to have left 185,000 murres (*Uria* spp.) dead and is likely to have suppressed the population for many years afterwards (Piatt and Anderson, 1996).

1.5.2. Marbled murrelet (*Brachyramphus marmoratus*)

Marbled murrelets are a widespread seabird along the western coast of North America, ranging from central California to Alaska (Speckman et al., 2000), with the majority of the population abiding in Alaska (Piatt and Naslund, 1995). However, they are less abundant than common murrelets. They are an endangered species in California and are classified as a species of special concern in Alaska (Speckman et al., 2000). During the breeding season marbled murrelets are piscivore, coastal divers and during winter they are pelagic divers (De Graaf et al., 1985). In both seasons they often forage opportunistically in nearshore waters on locally abundant fish species, including juvenile herring and juvenile salmon in coastal lakes (Rodway et al., 1992). In the breeding season marbled murrelets gather in near-shore waters and although during the winter individuals disperse hundreds of kilometres in all directions (Peery et al., 2006), they are rarely found further than 5km offshore (Rodway et al., 1992). Despite this winter is the best time to conduct censuses of marbled murrelets as during the summer the majority of the population nest in high trees in old-growth coastal forests (Speckman et al., 2000), within about 100km of the Pacific Ocean (Rodway et al., 1992). Marbled murrelets have a low reproductive rate as they lay only one egg per clutch, the population is therefore particularly susceptible to high adult mortality rates (Marshall, 1988). The availability of suitable nesting habitat may also play a role in regulating population size (Raphael et al., 2002) and an increase in the amount of edge in the forests due to extensive logging activities (Carter and Erickson, 1992) may have decreased marbled murrelet productivity (Nelson and Hamer, 1995). In fact due to logging, by 1988 less than eight hundred hectares of old-growth forest nesting habitat remained in Oregon (Marshall, 1988). In addition, gill-net mortality is a major threat to marbled murrelet populations in the North Pacific, this occurs when birds become tangled in fishing nets and drown, up to tens of thousands of individuals are killed in this way every year in Alaska alone (Carter et al., 1995a).

Survival rates of marbled murrelets have been shown to be positively correlated to the strength of the PDO index and mortality is lower during warm water years because they travel inland to breed less often and are therefore less vulnerable to predation (Peery et al., 2006).

1.5.3. Double-crested cormorant (*Phalacrocorax auritus*)

Double-crested cormorants are as widely distributed across the Pacific coast of North America as common murrelets and marbled murrelets, with breeding colonies inland and also along the coast (U.S. Fish and Wildlife Service, 2005). The Pacific coast of North America has two of the five recognised subspecies of double-crested cormorant (*P. a. cincinnatus* and *P. a. albociliatus*), which breed in Alaska and from British Columbia to Mexico respectively (Carter et al., 1995b). Hereafter both subspecies will be referred to as double-crested cormorant. These birds are predominately ground-nesters on cliff ledges and have a greater reproductive output than other seabirds used in this study, with an average clutch size of 3 or 4 eggs (U.S. Fish and Wildlife Service, 2005). Double-crested cormorant diet varies spatially and temporally but includes species such as Pacific herring, sandlance and salmonids (U.S. Fish and Wildlife Service, 2005). However, their foraging distribution is limited by the fact that their feathers are not waterproof and they must return to land daily to dry off (U.S. Fish and Wildlife Service, 2005). There are many factors that have historically limited the population of double-crested cormorants in the North Pacific, the most notable of which was contamination from DDE and DDT, which reduced their reproductive performance (Sydeman et al., 2001). Their range was also reduced by anthropogenic nest destruction and shooting of adult cormorants (U.S. Fish and Wildlife Service, 2005). However, populations have been recovering since the ban on DDT use in 1972 and the breeding population in California has subsequently doubled since 1990 (U.S. Fish and Wildlife Service, 2005). More recently, red foxes (*Vulpes vulpes*) were introduced to Oregon islands for use in hunting and in 2002 they destroyed double-crested cormorant eggs and chicks in the area (U.S. Fish and Wildlife Service, 2005). In addition, predation by bald eagles (*Haliaeetus leucocephalus*), glaucous-winged gulls (*Larus glaucescens*) and North-western crows (*Corvus caurinus*) have affected breeding colonies in British Columbia, Canada and Washington (Carter et al., 1995b). There is some evidence to suggest that environmental conditions can be a limiting factor to double-crested cormorant populations, with low reproduction rates linked to El Niño events (U.S. Fish and Wildlife Service, 2005). This study aims to investigate whether

there is also a link between double-crested cormorant populations and the phase of the PDO index.

1.6 Future Change

Anthropogenic induced climate change and atmospheric warming is expected to further compound this complex interplay between the PDO index and marine ecosystem responses, as white noise from atmospheric weather filters down to produce redder variability in biological systems (Doney and Sailley, 2013). The IPCC Fifth Assessment Report found that between 1971 and 2010, more than 60% of the global energy increase was stored in the upper oceans (IPCC, 2013). Warming of the upper ocean is likely to increase stratification which can inhibit the mixing of nutrients from the deep ocean and may lead to a reduction in overall ocean productivity (Overland et al., 2010). This has been evidenced by deepening of the mixed layer in the North Pacific, especially in the wake of the 1977 phase shift (Francis et al., 1998). Moreover, some marine ecosystems are predicted to experience a reduction in biomass of 19% to 29% due to the effects of climate change (Gu enette et al., 2014). However, warming sea surface temperatures (SSTs) also cause favourable wind conditions for upwelling in eastern boundary currents, this may go some way towards counteracting any decreases in biological productivity caused by stratification in the region (Overland et al., 2010). Another way increasing ocean temperatures could be somewhat beneficial to fish species is through swimming performance, as higher temperatures decrease the viscosity of the water and decrease drag on organisms (Drinkwater et al., 2010).

Whilst it is considered not possible to predict whether ENSO activity will be amplified or dampened by increasing SSTs in the Pacific Ocean (Collins et al., 2010), Pacific Decadal Oscillation patterns into the future may be considered by some as easier to forecast. As sea surface temperatures increase we could be expected to see prolonged warm phases of PDO and an associated reduction in plankton and fish populations. However, there is evidence which suggests that the pattern of PDO variability that occurred in the 1900s is likely to continue long into the 21st century even with the addition of an increasing sea surface temperature trend (Overland and Wang, 2007). In addition, Sydeman et al. (2013) concluded that the variance of the PDO index has not changed since 1985. Nevertheless, there is considerable concern that global warming may be

accelerated by a weakening of the Pacific trade winds and a return to warmer Pacific sea surface temperatures (Thompson et al., 2015). To this end there is a pressing need for the fishing industry to find ways to adapt to different fishing conditions and to reduce exploitation rates (Gu enette et al., 2014).

1.7 Relation to previously used methods

There have been several previous studies that have examined the 1977 and potential 1989 phase changes in Pacific Decadal Oscillation (PDO), sea surface temperature (SST) data and commercial fisheries catch data, using a wide variety of different statistical methods. One of the most extensive studies was produced by Hare and Mantua in 2000, they combined a total of one hundred climatic and biological timeseries, including fish recruitment and landings data in order to identify and calculate the average step magnitude of different regimes. In an earlier study Mantua and his colleagues used data of salmon catches and the PDO index to investigate the significance of these phase changes in PDO using intervention analysis, which is a version of a two sampled t-test and best-fit interventions for salmon data (Mantua et al., 1997). Previous statistical methods to analyse similar datasets also include principle component analysis (PCA) to summarise variability on fish catch only and catch and climate combined (Hare et al., 1999), generalized additive models (GAMs) for biological timeseries (Litzow et al., 2014) and linear regression for each species in each region and each regime period (Irvine and Fukuwaka, 2011). Therefore, there is a range of statistical methods available to analyse commercial fish landings timeseries data and to test hypotheses similar to those of this study. However, there has been a general lack of statistical analysis of seabird data from the North Pacific in relation to climatic forcing and especially the Pacific Decadal Oscillation index. The only study that could be found that uses Christmas Bird Count (CBC) data in this way was produced by Vandenbosch (2000) and was centred on seabird populations in Honolulu, Hawaii. This paper's methods included comparing average population sizes for 3 years before and after known ENSO events and regression analysis of dependence of seabird populations on the PDO index (Vandenbosch, 2000). This study will further develop the results of Vandenbosch (2000) and it will, for what is believed to be the first time, investigate the interplay between both fish species and bird

species with the PDO index over the whole stretch of the western North American coastline, from Alaska to California.

1.8 Likely impact of research

Research into this area of the Earth system is necessary to understand the changes occurring in the North Pacific, in the context of anthropogenic induced climate change. This research also has the potential to contribute to knowledge of changing ocean system teleconnections. Such findings are likely to have implications for the management of marine ecosystems and commercial fisheries in the Pacific Ocean, with global fish catches expected to decrease by approximately 5% to 48% into the future, due to the effects of global warming (Guénette et al., 2014).

2. Data sources and methods

2.1 Commercial fisheries

Data were obtained from the National Oceanic and Atmospheric Administration (NOAA) National Marine Fisheries Service (NMFS) commercial landings statistics. These data are available at: <http://www.st.nmfs.noaa.gov/commercial-fisheries/commercial-landings/annual-landings/index> (NOAA, 2015a). Data of commercial catches in metric tons were used because they are the longest and most continuous proxy available for species abundance in the region. The fish species chosen to use as a proxy in this study were: sardine (*Clupeidae spp*), Pacific herring (*Clupea pallasii*), coho salmon (*Oncorhynchus kisutch*), sockeye salmon (*Oncorhynchus nerka*), chum salmon (*Oncorhynchus keta*), Chinook salmon (*Oncorhynchus tshawytscha*) and pink salmon (*Oncorhynchus gorbuscha*) due to the relative continuity of these datasets from 1950 to 2012. In order to ensure the results were comparable between species landings recorded in the database as 'at sea process' (where some fish species are gutted or otherwise processed before crossing the dock) were omitted (NOAA, 2015b), as were data on herring caught using the roe on kelp method. All species data were summarised as total catch in metric tons per year and per Pacific coast USA state of California, Oregon, Washington or Alaska. Figure 8 is a map of sea surface temperature (SST) in the Pacific, showing how fish catch and sea surface temperatures were delineated for this study (using only the ocean area in each box), in each of these states. The box around the coastline of each state was designed to incorporate the Exclusive Economic Zone of 370km from the shoreline, in order to include all fish caught within this area (United Nations, 2013). Years when less than 0.1 of a metric ton of any fish species were caught were classified as a catch of 0 metric tons. Years when no data were available were not classified as missing data because, under those parameters, the statistical tests could not be calculated. Therefore, these years were assumed to represent when no fish were caught. This was considered to be a reasonable assumption as values of zero are not recorded in the dataset and landings statistics are continually being updated.

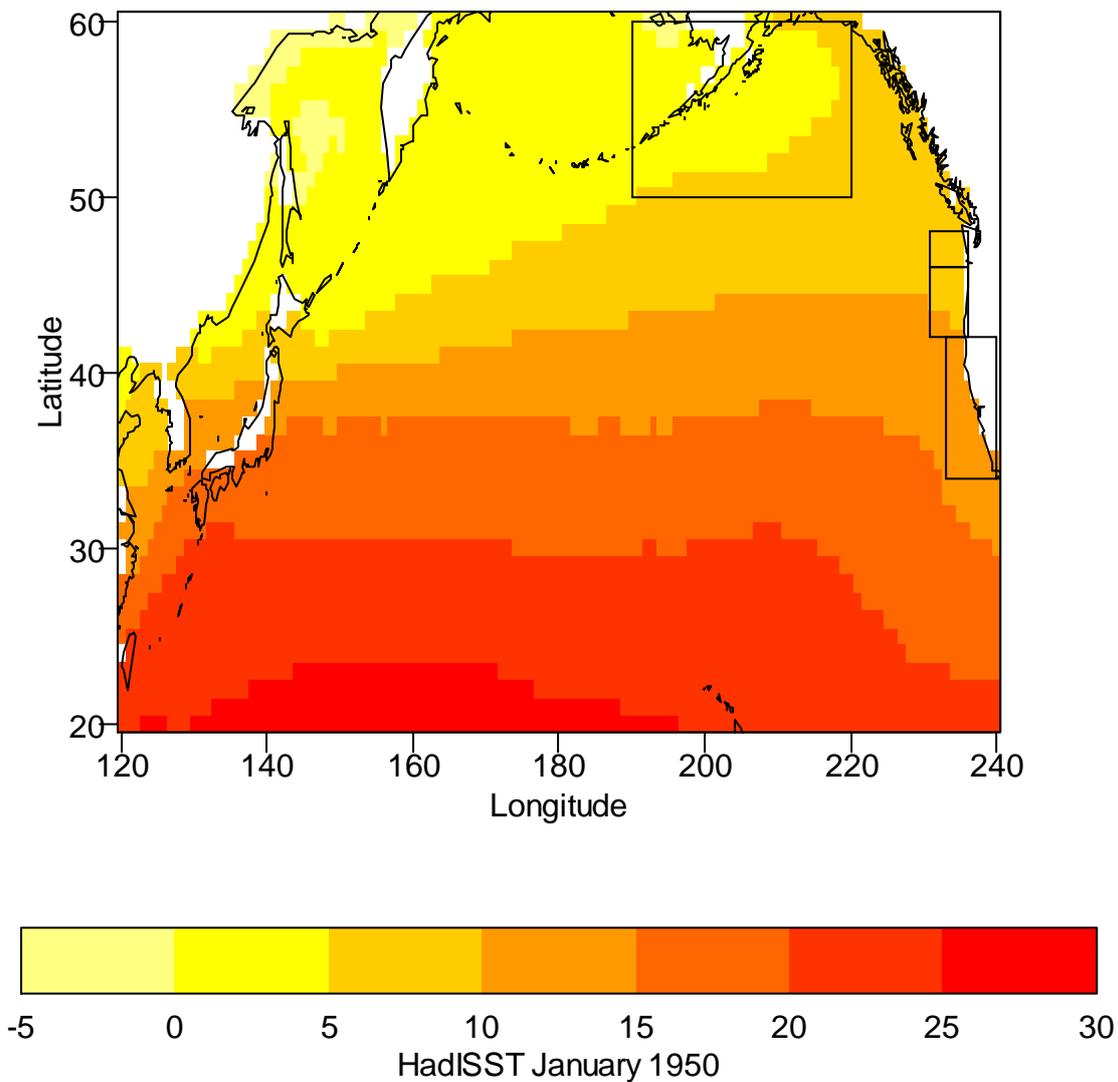


Figure 8. Map of the Pacific region showing SST data from January 1950 from the HadISST dataset. Black boxes represent (from North to South) the areas of Alaska, Washington, Oregon and California

2.2 Macrozooplankton biomass

Data on zooplankton biomass came from the California Cooperative Oceanic Fisheries Investigation (CalCOFI) website and are available at: <http://www.calcofi.org/new.data/index.php/zooplankton/zooplankton-data> (CalCOFI, 2015). These biomass values are reported as wet displacement volumes in cm^3 per 1000m^3 strained, using a 71cm diameter paired bongo net. Annual averages from 1951 to 2012 were calculated from this data and they were rounded to two decimal places for accuracy for the purposes of this study.

Where there is no data present for a year it is assumed that no surveys were conducted, this is represented by values of NA in the dataset.

2.3 Seabird abundance

Data were acquired from the Christmas Bird Count (CBC) Historical Results, available at: <http://www.christmasbirdcount.org> (National Audubon Society, 2015). Bird counts are conducted by volunteers each year between the 14th December and the 5th January. The volunteers follow specified routes within a circular area with a 24km diameter. All birds they either see or hear in this circle in a 24 hour period are recorded, giving an indication of the number of birds in a study area on that day. The number of birds recorded per party hour (number of birds seen divided by total party hours in the field) in each study circle in each year were averaged by U.S. state of California, Washington, Oregon or Alaska. These values were used as a proxy for species abundance in order to allow for variation in survey effort between count locations and years.

The online database was queried for data on non-migratory seabird species that were considered to be good indicators of climatic forcing and that had fairly consistent records as far back as 1950 along the length of the Pacific coast of North America. As such, data were obtained for common murre (*Uria aalge*), marbled murrelet (*Brachyramphus marmoratus*) and double-crested cormorant (*Phalacrocorax auritus*) from 1950 to 2012, in California, Oregon, Washington and Alaska.

2.4 Climate indices

2.4.1 PDO index

Values of the Pacific Decadal Oscillation (PDO) index were obtained from: <http://jisao.washington.edu/pdo/PDO.latest> (Mantua, 2015). This timeseries is composed from a variety of data sources and is adjusted so that monthly global sea surface temperature (SST) anomalies are removed and therefore, the PDO index is separated from the global warming signal that may be present in the data. Before performing statistical tests on this data the monthly values were averaged to produce a dataset of annual PDO index from 1950 to 2012. In addition, a winter PDO index was produced as an average of the months of December, January and February in each year.

2.4.2 Hadley Centre sea ice and SST dataset (HadISST)

This dataset is a combination of sea ice concentration and importantly for this study, globally complete monthly SST values from 1870 to present. It is available from: <http://www.metoffice.gov.uk/hadobs/hadisst/> (Rayner et al., 2003). In the statistical programme R, this data was spatially confined to the study area in the North Pacific and shortened so that it began in 1950 and ran for the same period of time as there is fish and bird population data. The data were also subsequently divided by region to produce a sea surface temperature (SST) dataset for each state along the west coast of North America, in order to perform regional statistical tests. These datasets of HadISST of each state and the average of all states combined were then adjusted so that the seasonal cycle was removed from the data in one instance and in the other the long-term warming trend was removed. Therefore, six different datasets were produced from HadISST, one of the raw values, one with seasonal cycle removed and one with the warming trend extracted, each were averaged over all states and in each state separately.

2.5 Statistical analysis

Data analysis for all species of birds and fish were completed in the statistical programme R (R Core Team, 2014), unless otherwise stated.

2.5.1 Distribution of the data

Initially, the timeseries data were visually inspected using histograms. Shapiro-Wilk tests were then conducted which confirmed that most species in most states were not normally distributed and instead significantly right-skewed. Square-root and log transformations were performed on the data in order to make them conform to a normal distribution, so that parametric statistics could be used. However, even with these transformations some distributions of fish and bird species in some states remained non-normal. In addition, it has been recommended that count data such as numbers of individuals of species should not be log transformed because they may contain many observations of zero and some missing values (O'Hara and Kotze, 2010). In light of this and because transforming the data did not result in the non-normal data conforming to a normal distribution, non-parametric tests were subsequently conducted on all data.

2.5.2 Tests of presence and significance of regime shifts

Firstly, the pattern of species population changes over time were displayed in stacked area graphs produced in Microsoft Excel. To test for the presence or absence of regime shifts in the North Pacific ecosystem in 1977 and 1989, multiple Wilcoxon rank sum tests were conducted on all species in all states and in each state separately. These tests analyse whether there is a significant difference between the medians of two groups, before and after each alleged regime shift in 1977 and 1989 and therefore whether they are likely to have come from different populations. Wilcoxon rank sum tests were also performed to test for differences between these times in the PDO index itself. The same test was then conducted to investigate whether the two 'cool' PDO phases from 1950 to 1977 and 1989 to 2012 were significantly different from the 'warm' phase of the PDO from 1978 to 1988. This Wilcoxon rank sum test between 'cool' and 'warm' periods was also run with species data to determine whether these periods were statistically different in the North Pacific ecosystem. Box-and-whisker plots were drawn up to illustrate the results of these tests graphically.

2.5.3 Tests for significant trends between regime shifts

Wilcoxon rank sum tests indicated whether shifts in 1977 and 1989 did occur in both the climate indices and species population sizes, but it is also important to understand whether populations were increasing or decreasing before and after these shifts, in order to conclude what effect the phase of the PDO index has on the North Pacific ecosystem. Mann-Kendall tests were therefore conducted in R using the Kendall package (McLeod, 2011), to identify the presence or absence of negative and positive trends in species populations, the PDO index and SST data over the three PDO phase periods 1950 to 1977, 1978 to 1988 and 1989 to 2012. The Mann-Kendall test is a non-parametric trend test that indicates whether values of the response variable tend to increase or decrease over time, it produces p-values to allow for the identification of statistically significant trends (Helsel and Hirsch, 1992). This test is not suitable for data with cyclical patterns, such as those present in the Pacific Decadal Oscillation index (Kufs, 2011). However, it has been adapted for use on this data by calculating the test separately for each stage in the cycle (for each 'warm' or 'cool' phase of the PDO index) (Kufs, 2011).

2.5.4 Explaining variations in bird and fish populations

The last line of enquiry of interest to this study was what factors or variables can best explain variations in fish and bird population sizes in the North Pacific over time. Linear models were fitted to the data of each bird and fish species, in each state and in all states combined, to examine whether the PDO index had a greater influence on population size than sea surface temperature data, or whether population sizes of other species and inclusion of lag times could better explain variations than regional climate indices.

To investigate this several different linear models were run on the data from 1950 to 2012, with a range of variables combined. These models were initially run for each state and for all regions combined without the influence of a climate index, to see whether populations of other birds and fish could explain some population variations in a single species. Additionally, this set of linear models was re-run to investigate effects of competition on population sizes, with models analysing a bird species against all other bird species and one fish species against all other fish species. In the second linear models run, the PDO index was included together with the variables explained above. Then, years with a value of zero bird species sighted, fish caught or zooplankton biomass netted were excluded from the linear models and they were run again, as before. In the fourth round of linear models time lags were included to account for the response times of different trophic levels, so that initially bird populations were lagged one year behind fish populations and the PDO index. A second set of these linear models were run which lagged bird populations two years behind PDO index and fish populations lagged one year behind PDO index. For the final round of linear models sea surface temperature (SST) data replaced the PDO index as the climatic factor. These models were run with the HadISST dataset for the period 1950 to 2010, first with the seasonal cycle in the HadISST data removed and then with the long-term warming trend removed.

3. Results

Figure 9 shows a stacked area graph of the raw data for all fish species used in this study, across all U.S.A. Pacific states (California, Oregon, Washington and Alaska). Therefore, the complete height of the graph represents total commercial catch in metric tons between 1950 and 2012. There was a sharp increase in commercial catch (as a proxy for population size) which began before 1977 and is probably associated with a phase change of Pacific Decadal Oscillation at this time, this population increase continued until approximately 1980. This increase appears to be mainly concentrated in pink and sockeye salmon and herring populations, with chum, Chinook and coho salmon changing little over this period. After 1980 populations of all species levelled off and from figure 9 there is little to suggest that commercial catch rate, or species population sizes responded to a change in phase of the PDO index in 1989. However, this has been further investigated using statistical techniques to test the hypotheses presented in scientific papers that there was a change from a positive to a negative sign of the PDO index in 1989 (Hare and Mantua, 2000) and that biological populations showed a response to this (Benson and Trites, 2002; Hare and Mantua, 2000; Sydeman et al., 2001).

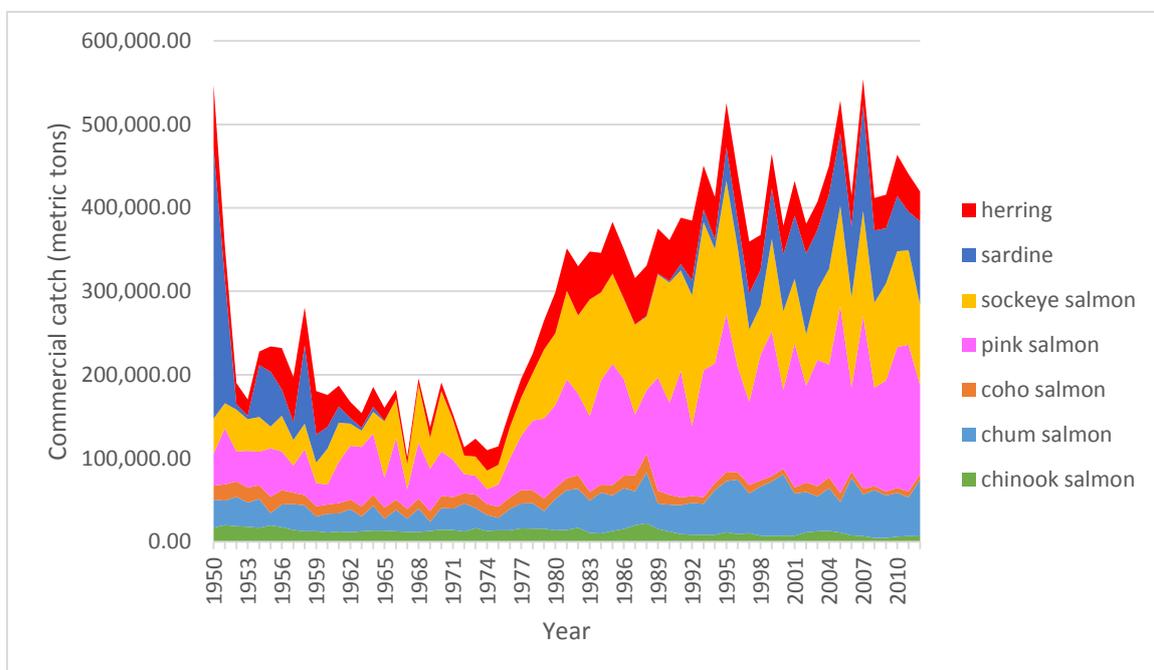
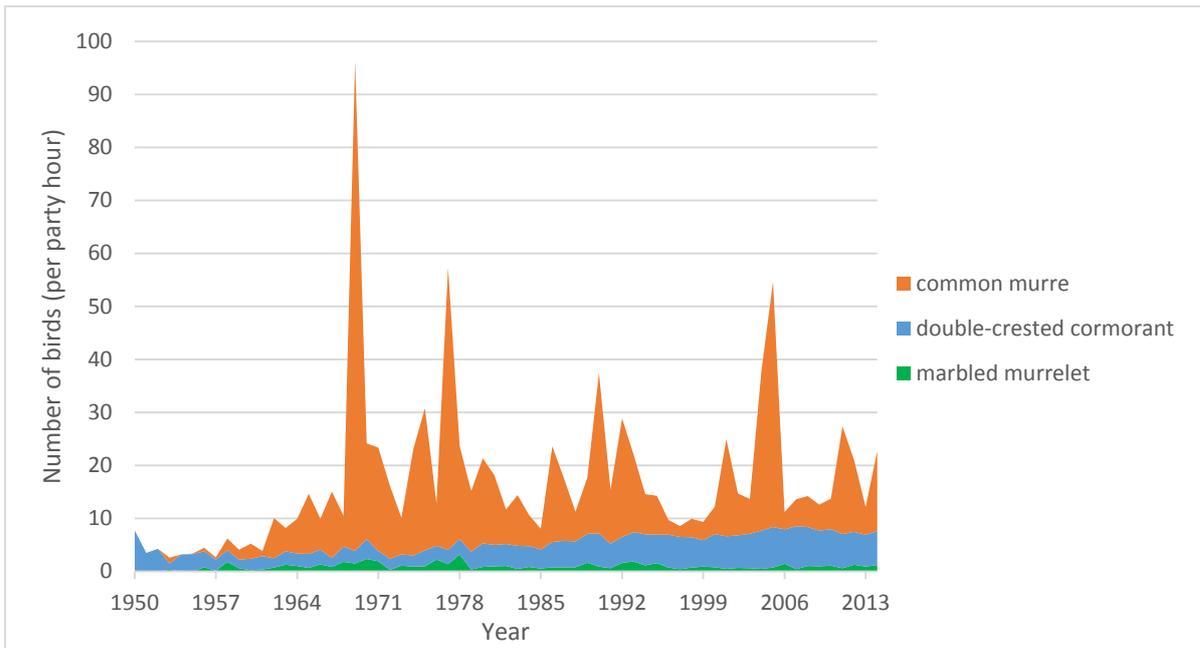


Figure 9. Stacked area graph showing the contribution of each fish species (in metric tons) used in this study to total commercial catch across all states

For the three species of bird used in this study (common murre, marbled murrelet and double-crested cormorant) the stacked area graph (see figure 10a) has a lot more variability than that of fish populations (see figure 9). The majority of this variability in figure 10a comes from common murre sightings that range from less than ten in some years to ninety two in 1969. As such, there is no discernible temporal pattern in total bird populations, in this graph. Figure 10b shows that when marbled murrelet and double-crested cormorant sightings are separated from those of common murre, double-crested cormorant shows an increasing trend from 1950 to 2014. However, from figure 10b it is difficult to ascertain whether either bird species showed any response in population size to the reported PDO phase changes in 1977 and 1989.

(a)



(b)

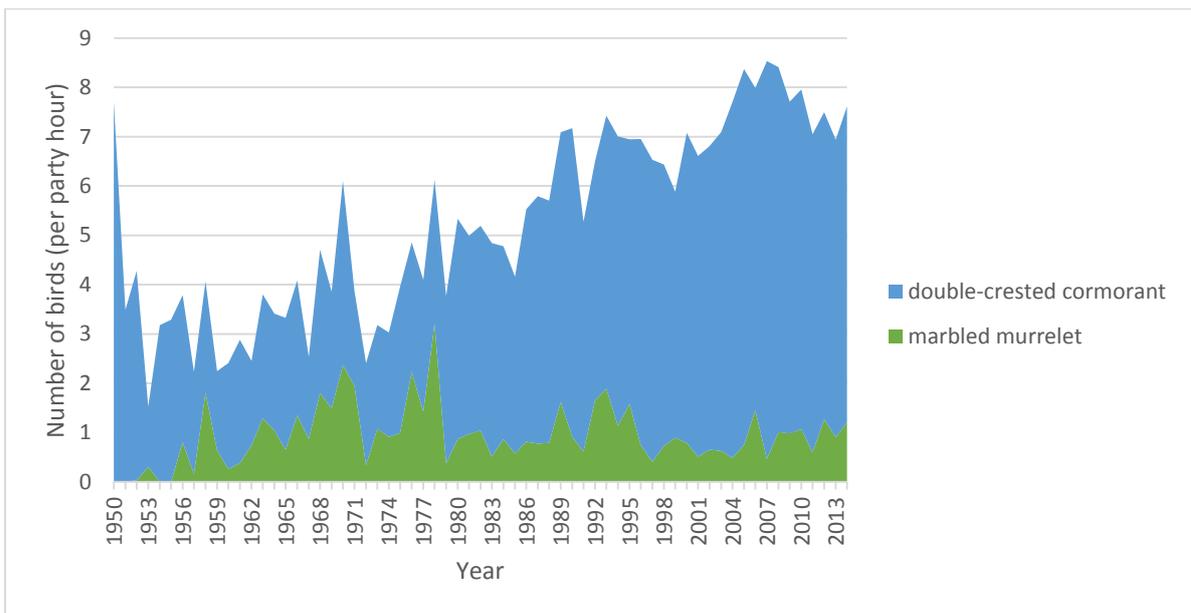


Figure 10. Stacked area graphs showing (a) the contribution of common murre, marbled murrelet and double-crested cormorant (in number of birds per party hour) to total sightings across all states and (b) contributions of double-crested cormorant and marbled murrelet only

Figure 11 is a graph displaying the four different climate indices from the North Pacific used in this study to explain variations in fish and bird populations. As

expected both graphs of annual and winter Pacific Decadal Oscillation index (figures 11a and 11b) showed substantial increases in 1977 associated with the shift to a positive or 'warm' phase of the PDO index. What is interesting about this change is that from figures 11a and 11b the PDO index appears to start increasing before the red line, which represents 1977. These graphs therefore suggest that there was a long transition period in the PDO index over about ten years, which started in approximately 1972 and continued until the mid-1980s. These graphs also show a decrease around the second red line in 1989 when there was a potential return to a negative or 'cool' phase of the PDO index. However, the graph of the annual PDO index (figure 11a) shows a larger decrease in the index from 1999 to 2000 than in 1989. This further fuels debate as to the significance of the decrease in 1989 and whether it constitutes a phase change in the PDO index.

Sea surface temperature (SST) values were used from the HadISST dataset, figure 8c shows seasonal cycle removed from this data and figure 11d is without the long-term warming trend, the black line represents the average of the whole North Pacific (including the western extent, along the coasts of Asia and Russia) and each coloured line is a different USA Pacific state. These graphs show that the relationship between PDO phase shift years and SST in this region is less distinct than with the PDO index. Nevertheless, from figures 11c and 11d it is possible to discern an increase in SSTs in all states immediately preceding and during the more major 1977 phase change of the PDO index. Similarly to the graphs of the PDO index, figures 11c and 11d suggest that this was an approximately ten year transition period of sea surface temperature, from a 'cool' to a 'warm' state, between about 1971 and the mid-1980s. There was no apparent decrease in temperatures as a response to the potential PDO phase change in 1989. Additionally, average HadISST values over the whole North Pacific area did not respond to phase changes of the PDO index in either 1977 or 1989.

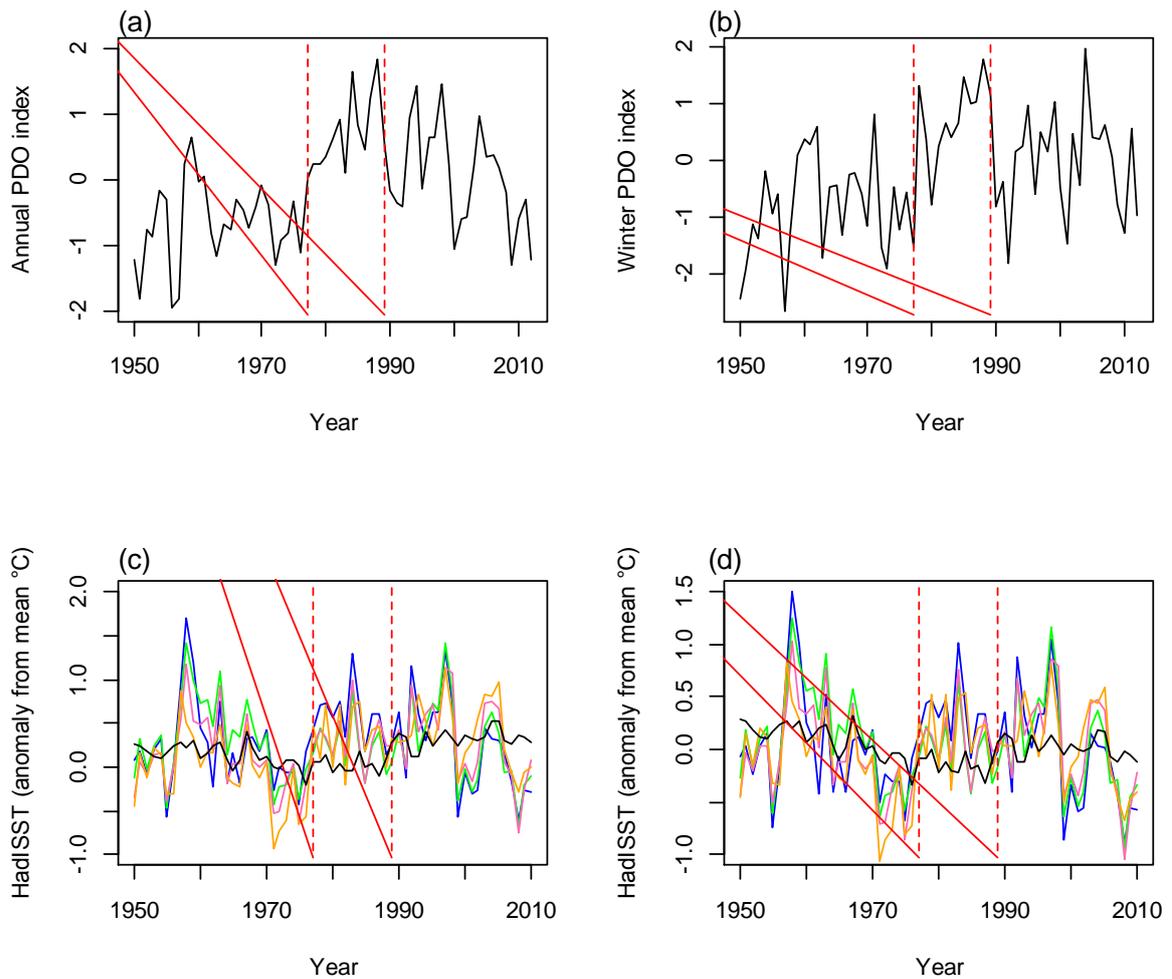


Figure 11. Graphs of climate indices used in this study annual (a) and winter (b) Pacific Decadal Oscillation index and HadISST data with seasonal cycle removed (c) and warming trend removed (d), black line is average SST over the whole North Pacific, blue line is in California, green line is Oregon, pink line is Washington and orange line is Alaska. Vertical red lines in all plots indicate potential PDO phase change years of 1977 and 1989.

3.1 Tests for significant differences in medians of bird and fish populations between PDO phases

3.1.1 Fish species

When all the states were combined, Wilcoxon's rank sum tests showed that the majority of the fish species and zooplankton in the North Pacific displayed a significant difference in population size before and after the 1977 change from

negative to positive phase of the PDO index (see figure 12 and figure 13). The exception to this was sardine, which had a p-value of 0.18 and therefore appears to show no change in population size around 1977, this can be seen in figure 13a, as the box and whisker plot shows the medians of the population before and after 1977 were virtually identical. Separating these results by state and with a 95% confidence level, revealed that all species in all states displayed a significant difference in population size before and after the 1977 event, apart from sardine in California, Chinook salmon in Alaska and pink salmon in California.

The results of Wilcoxon's rank sum tests on a difference in fish populations before and after the 1989 shift of the PDO index were more varied than that of 1977. In all states sardine, coho salmon, sockeye salmon, Chinook salmon and pink salmon showed a significant difference, whereas herring (figure 13b) and chum salmon (figure 12c) did not. Results were also not significant for herring and coho salmon in Alaska, chum salmon in Washington, pink salmon in Oregon and Washington and zooplankton in California.

Wilcoxon's rank sum tests were also conducted to examine whether there were significant differences in fish populations between 'warm' and 'cool' phases of the Pacific Decadal Oscillation (PDO) index. Amongst the eight fish species tested in all states combined, there was an even split of four species that showed a significant difference- sardine, herring, coho salmon and chinook salmon and three species that did not- sockeye salmon, chum salmon and pink salmon, as well as zooplankton (see figure 12 and figure 13). There was a similarly large mix of results when each fish species was divided into the four different states. Herring displayed a significant difference in population size between the phases of the PDO index in all but Washington, while coho salmon and Chinook salmon populations were not significant in California, Oregon or Washington, but were significant in Alaska. Sockeye salmon did not show a significant difference in relation to PDO phases in any of the states and chum salmon only produced a significant result in Washington. Similarly pink salmon only displayed a significant difference in populations in California.

Wilcoxon's rank sum tests on significant differences in fish populations between the two 'cool' phases of Pacific Decadal Oscillation before 1977 and after 1989, revealed that all species in all states combined had a significant population

difference, apart from coho salmon. For example, Chinook salmon populations (figure 12d) clearly displayed a significant difference between cool PDO periods in 1950 to 1977 and 1989 to 2012 and the warm phase in 1978 to 1988, whereas the box and whisker plot of coho salmon (figure 12a) shows an overlap in the population distributions of these time periods. When these results were divided into separate states an interesting consensus emerged, all populations of fish species in each state showed a significant difference between the two cool PDO phases apart from herring in Oregon and pink salmon in California.

When all species of fish (coho, Chinook, chum, sockeye and pink salmon and sardine and herring) in all states were combined to create a timeseries of total commercial catch, Wilcoxon's rank sum tests showed that both the 1977 and 1989 PDO phase shifts were highly significant, with p-values of <0.01 . Figure 13c displays this total fish timeseries as a box and whisker plot which shows a stepwise increase in commercial catches, as a proxy for population size over the whole time period. A Wilcoxon's rank sum test also revealed that with a p-value of 0.91 there is no significant difference between fish species population sizes during 'warm' and 'cool' PDO phases, that is, 'cool' periods from 1950 to 1977 and 1989 to 2012 are not significantly different from the 'warm' PDO period between 1977 and 1989. This result can clearly be seen in figure 13c, which shows a step-wise increase in fish catch over time and illustrates that the distribution of total fish populations in the 'warm' PDO period after 1977, lies between those of the two cooler PDO periods.

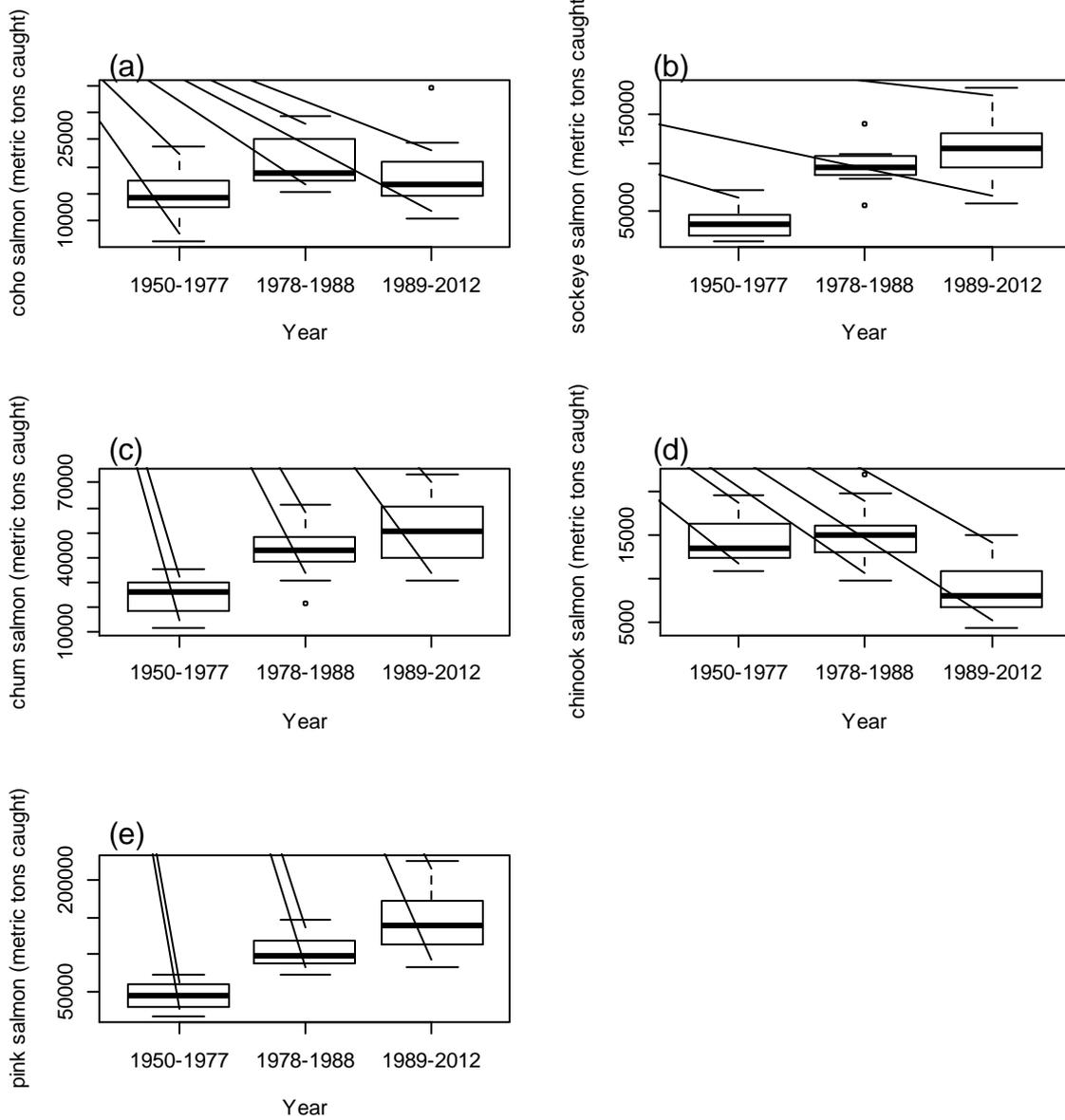


Figure 12. Box and whisker plots showing quantities of coho salmon (a), sockeye salmon (b), chum salmon (c), Chinook salmon (d) and pink salmon (e) caught in all states in metric tons over three time periods, 1950 to 1977, 1978 to 1988 and 1989 to 2012.

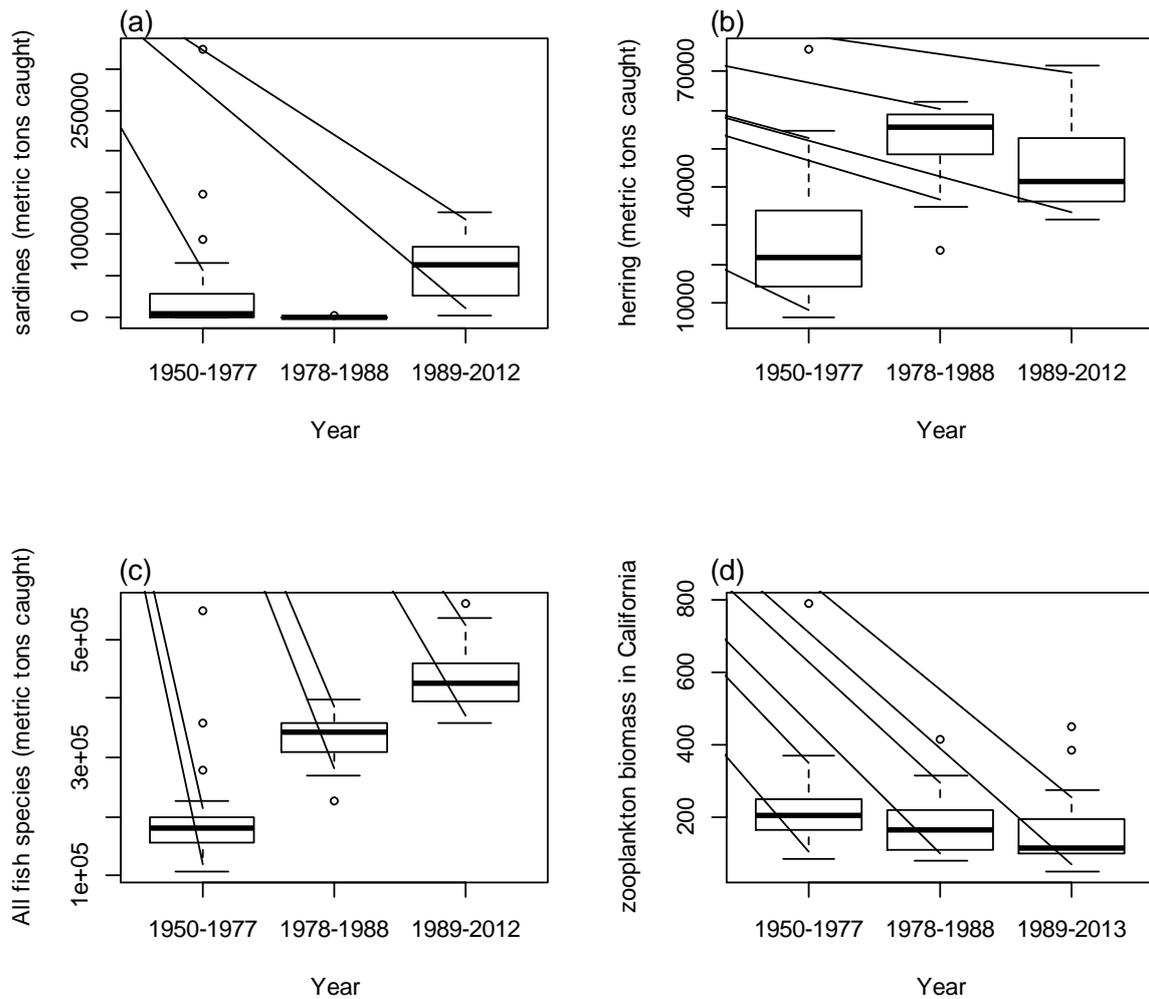


Figure 13. Box and whisker plots showing quantities of sardine (a) and herring (b) caught in all states in metric tons, all fish species in all states combined (c) and zooplankton biomass in California (d) over three time periods, 1950 to 1977, 1978 to 1988 and 1989 to 2012.

3.1.2 Bird species

Results of Wilcoxon's rank sum tests on common murre, marbled murrelet and double-crested cormorant populations before and after the 1977 and 1989 phase changes of Pacific Decadal Oscillation (PDO) were highly varied. The results of these statistical tests are illustrated as box and whisker plots in figure 14, showing how the population size of each species changes in all states combined. At a confidence level of 95% (p -value= 0.05), both common murre and marbled murrelet were shown to exhibit no significant difference between

population sizes after the 1977 and 1989 shifts when all states were combined. Figures 14a and 14b show that the populations in all three time periods overlap considerably. However, when each state was considered separately a different pattern of significant changes in population size emerged, with common murre showing significant differences in population size after the 1977 shift in all states. The response to the potential change of the PDO phase in 1989 was less clear cut as there was no significant difference in population size after the event in Oregon and Alaska, but there was a significant difference at this point in California and Washington.

For marbled murrelet populations in North America, there was a similar response to each of the events in the PDO index in 1977 and 1989, with some states having a significantly different population size in each case. However, these states changed, as in 1977 there was a significant response in California, Oregon and Alaska and in 1989 there were changes in Washington and Alaska. Contrary to the other two bird species studied double-crested cormorant in all states showed significant differences in population size at both the 1977 and 1989 dates.

Tests for significant differences of bird populations between 'warm' and 'cool' phases of the Pacific Decadal Oscillation (PDO) index also produced a range of results. Wilcoxon's rank sum tests were conducted on each species in each state to compare population dynamics of 1950-1977 and 1989 to 2014 ('cool' PDO phases) against those from 1978 to 1988 ('warm' PDO phase). When all the states were combined there was no significant difference in populations of common murre, marbled murrelet or double-crested cormorant between positive and negative phases of the PDO. The spatial pattern of data from each state individually generally confirmed this, although there were significant differences for common murre and marbled murrelet in California and Washington and for double-crested cormorant in Alaska.

Further Wilcoxon's rank sum tests were conducted to investigate whether there were differences in bird populations between the two recent 'cool' periods of the PDO from 1950 to 1977 and from 1989 to 2014. As was expected there was no significant difference between these periods when all the states were combined for common murre (figure 14a) and marbled murrelet (figure 14b). However, double-crested cormorant displayed a significant difference in population size

between the two negative phases of the PDO (figure 14c), with every state having a p-value of less than 0.01. Figure 14 clearly shows that double-crested cormorant has a distinctly different population distribution over time than that of common murre and marbled murrelet. Each of the three time periods in figure 14c has a different median from one another, whereas for marbled murrelet the pre-1977 period has a different distribution to the two later ones and for common murre, population size appears to have changed little between 1949 and 2014.

When all three species of birds (common murre, marbled murrelet and double-crested cormorant) were combined across all states there was a large amount of overlap in population size between the time periods (see figure 14d). Despite this, a Wilcoxon's rank sum test showed that there was a significant difference in bird populations before and after 1977, with a p-value of <0.01 . However, the potential PDO phase change in 1989 was not associated with a significant change in bird populations (p-value= 0.79). There was also no significant difference in total bird population size between 'warm' and 'cool' phases of the Pacific Decadal Oscillation, this result matches that of total fish populations.

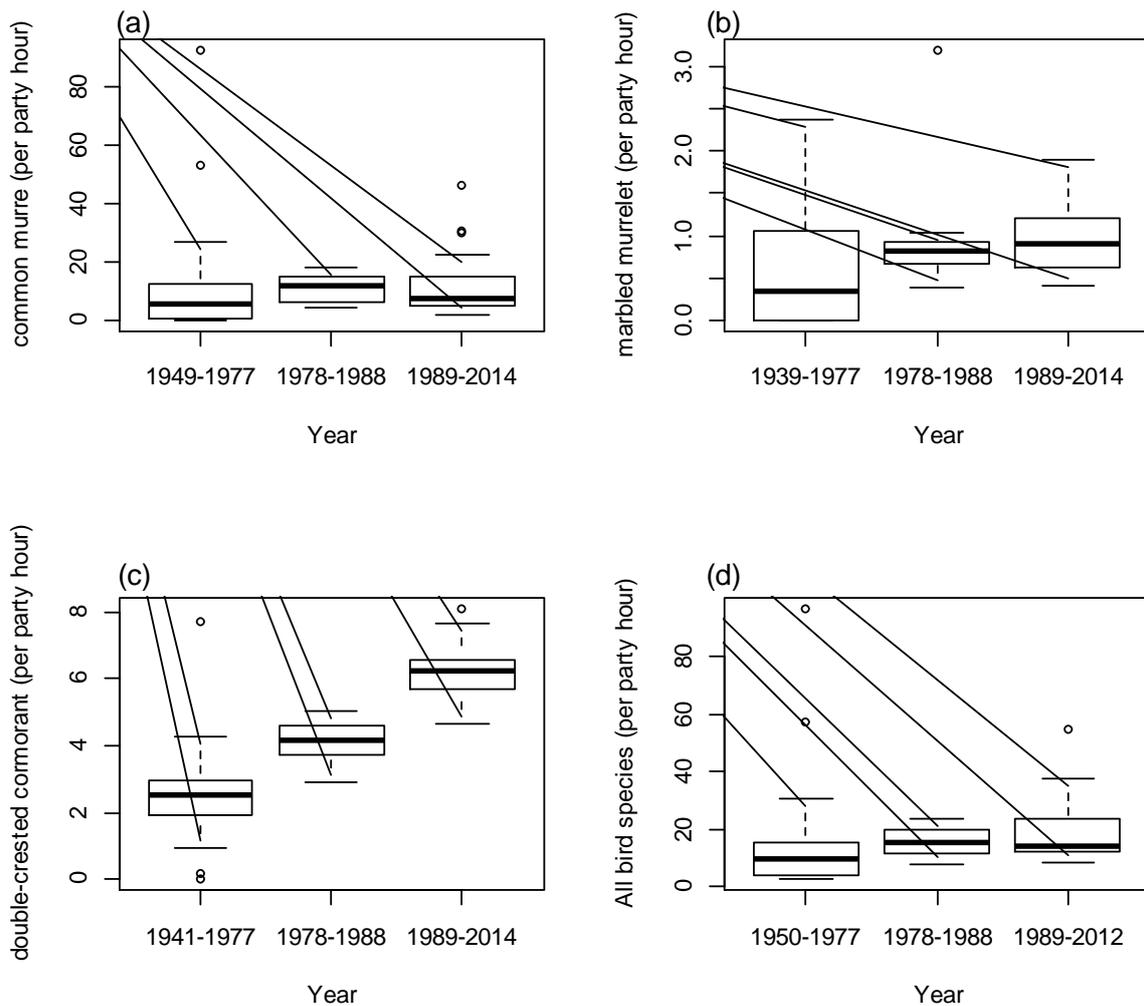


Figure 14. Box and whisker plots of common murre (a), marbled murrelet (b), double-crested cormorant (c) and all three species of birds combined (d) showing the difference in population size over three time periods, pre-1977, 1978 to 1988 and 1989 to 2014

3.2 Mann-Kendall tests for significant trends

3.2.1 Climate indices

To expand on the results of Wilcoxon's rank sum tests that investigated whether a population was statistically different between time periods, Mann-Kendall tests were used to identify statistical trends, in order to be able to state whether climate indices, fish and bird populations were increasing or decreasing within these time periods.

Mann-Kendall tests were therefore used to identify the presence of positive and negative trends in the Pacific Decadal Oscillation index (both annually and as a winter value) and the HadISST dataset during three time periods: 1950 to 1977, 1978 to 1988 and 1989 to 2012. Table 1 shows the results of these tests, with the reported test statistics and p-values. The trend was considered to be statistically significant with a p-value of equal to, or less than 0.05. It is clear from these results that there was a positive trend in the PDO index between 1978 and 1988, which shows that the PDO was warming during the positive phase both annually and over the winter months. After the 1989 shift this warming was reversed in the annual PDO index, confirming that it entered a negative or 'cool' phase and continued to decline, perhaps until 2012. However, the winter index shows no trend over this time period. For the HadISST dataset, both with the seasonal cycle removed and the long-term warming trend removed there were significant negative trends before 1977, indicating a negative phase of the PDO index, but there were no significant trends in SST thereafter.

Table 1. Mann-Kendall test results showing test statistics and p-values for climate indices

Climate index	Mann-Kendall test results					
	1950-1977		1978-1988		1989-2012	
	test stat	p-value	test stat	p-value	test stat	p-value
Annual PDO	0.10	0.49	0.56	0.02	-0.28	0.05
Winter PDO	0.08	0.54	0.53	0.03	-0.03	0.86
HadISST cycle removed	-0.46	<0.01	-0.05	0.88	0.10	0.54
HadISST trend removed	-0.56	<0.01	-0.20	0.44	-0.24	0.13

3.2.2 Fish species

Mann-Kendall test results for salmonid fish species in the three regime periods across the Pacific region were highly varied. Table 2 shows that when all states were combined before 1977 and between 1978 and 1988 only chum salmon had a significant trend and this was negative and positive respectively. After the 1989 shift in the PDO index, Chinook and coho salmon had negative trends and chum salmon showed a positive trend. These results generally correlate with

those of the PDO index which showed a positive trend after 1977 and a negative one after 1989.

When these results were analysed by region they showed even greater variability, before 1977 there was no discernible overall pattern, although there was no trend in Washington for any of the five salmon species. After the climatic event in 1977 the majority of the species in each state showed no trend, with significant results in only coho salmon in California which showed a negative trend, Chinook salmon in Alaska also with a negative trend and sockeye salmon in Oregon with an increasing, positive trend. After 1989 there were more significant trends when each species in each state was considered than after 1977, trends of all species in California were negative, indicating declining populations of coho, Chinook and pink salmon. In Oregon and Washington the majority of salmonid species showed no significant trend. The exception was sockeye salmon that had an increasing population in Oregon and a decreasing trend in Washington between 1989 and 2012. In Alaska, coho and Chinook salmon showed a negative trend, chum salmon had a positive trend and pink and sockeye salmon had no significant trend. Overall, table 2 shows these results were very variable and they display no obvious spatial pattern across the states of North America.

Table 2. Mann-Kendall test results showing test statistics and p-values for salmonid fish species in all states and each region separately

Species	Location	Mann-Kendall test results					
		1950-1977		1978-1988		1989-2012	
		test stat	p-value	test stat	p-value	test stat	p-value
coho salmon	All states	0.03	0.83	0.31	0.21	-0.51	<0.01
	California	0.51	<0.01	-0.49	0.04	-0.52	<0.01
	Oregon	0.44	<0.01	-0.02	1.00	-0.11	0.47
	Washington	0.20	0.14	0.05	0.88	0.01	0.98
	Alaska	-0.41	<0.01	0.46	0.06	-0.47	<0.01
sockeye salmon	All states	-0.05	0.71	0.38	0.12	-0.28	0.06
	Oregon	-0.46	<0.01	0.60	0.02	0.52	<0.01
	Washington	0.07	0.59	0.13	0.64	-0.52	<0.01
	Alaska	-0.05	0.74	0.31	0.21	-0.25	0.10
chum salmon	All states	-0.27	0.05	0.56	0.02	0.29	0.05
	Oregon	-0.71	<0.01	0.18	0.48	-0.41	0.01
	Washington	-0.17	0.21	0.42	0.09	-0.03	0.86
	Alaska	-0.23	0.09	0.46	0.06	0.31	0.03
Chinook salmon	All states	-0.22	0.11	0.13	0.64	-0.44	<0.01
	California	-0.31	0.02	0.35	0.16	-0.32	0.03
	Oregon	-0.15	0.26	0.24	0.35	-0.11	0.47
	Washington	0.04	0.77	0.02	1.00	0.09	0.57
	Alaska	-0.33	0.01	-0.53	0.03	-0.42	<0.01
pink salmon	All states	-0.08	0.57	0.02	1.00	0.10	0.50
	California	0.48	<0.01	-0.04	0.93	-0.39	0.03
	Oregon	0.33	0.02	-0.14	0.62	-0.23	0.17
	Washington	-0.07	0.62	-0.24	0.35	0.06	0.71
	Alaska	-0.01	0.95	0.09	0.76	0.10	0.50

For the non-salmonid species (sardine, herring and macrozooplankton) there were more significant trends than the species of salmon (see table 3). Zooplankton in California showed no significant trends in any of the time periods. In all states, herring populations showed the same pattern as the PDO index of a cyclical negative, positive and negative trend. Whereas sardine showed an increasing population trend after 1989, both in California and when

all states were combined, herring consistently showed a negative trend across every state.

Overall, when all fish species from table 2, sardine and herring in every state were combined only the pre-1977 period showed a significant (negative) trend. This is surprising as based on the stacked area graph (figure 9), the Mann-Kendall test would be expected to show a significant positive trend after 1977. Table 3 shows that there was no significant trend between 1978 and 1988 in all fish species with a p-value of 0.06 and a test statistic of 0.46. This result was likely due to total population sizes rising sharply after 1977 and then slightly decreasing between 1985 and 1988 (see figure 9) and the Mann-Kendall test becomes weak with cyclical data. This was confirmed by conducting the test again with data from 1978 to 1985 only, which showed a highly significant (p-value < 0.01) positive trend that correlates to the sharp increase in fish populations seen in figure 9.

Table 3. Mann-Kendall test results showing test statistics and p-values for non-salmonid fish, all fish species combined and zooplankton

Species	Location	Mann-Kendall test results					
		1950-1977		1978-1988		1989-2012	
		test stat	p-value	test stat	p-value	test stat	p-value
sardine	All states	-0.77	<0.01	0.42	0.09	0.65	<0.01
	California	-0.77	<0.01	0.42	0.09	0.33	0.03
herring	All states	-0.41	<0.01	0.60	0.01	-0.43	<0.01
	California	-0.24	0.07	0.35	0.16	-0.75	<0.01
	Oregon	0.47	<0.01	0.67	<0.01	-0.57	<0.01
	Washington	0.51	<0.01	-0.60	0.01	-0.64	<0.01
	Alaska	-0.47	<0.01	0.67	<0.01	-0.29	0.05
All species	All states	-0.48	<0.01	0.46	0.06	0.27	0.07
zooplankton	California	-0.07	0.67	0.27	0.27	-0.06	0.71

3.2.3 Bird species

Table 4 shows that in all states both common murre and marbled murrelet had a significant positive trend in population sizes before the 1977 North Pacific event, but after this they showed no trend response to the 1989 phase change. When divided into states separately, common murre showed an overall pattern of a positive trend before 1977 and no significant trends thereafter, the same is

true of marbled murrelet in Washington and Alaska. However, marbled murrelet in California had a decreasing trend after the 1977 phase shift and in Oregon there were no significant trends at all.

Moreover, double-crested cormorant in all states combined showed no trend before 1977 and significant positive trends both before and after 1989, indicating consistent increasing population size since 1978. For double-crested cormorant the results in each state were much more variable than those of common murre and marbled murrelet. Notably, there was a negative trend in California before 1977 and a positive one after 1989 and in Washington there were increasing population trends after both the 1977 and 1989 phase shifts of the PDO. Overall, when all three species of birds in all states were combined there was only one positive trend (see table 4) and this was in the pre-1977 time period.

Table 4. Mann-Kendall test results showing test statistics and p-values for bird species in all states and each region separately

Species	Location	Mann-Kendall test results					
		1950-1977		1978-1988		1989-2012	
		test stat	p-value	test stat	p-value	test stat	p-value
common murre	All states	0.73	<0.01	-0.24	0.35	-0.06	0.71
	California	0.63	<0.01	-0.16	0.53	-0.17	0.24
	Oregon	0.55	<0.01	0.20	0.44	0.18	0.24
	Washington	0.42	<0.01	-0.13	0.64	-0.49	<0.01
	Alaska	0.56	<0.01	-0.13	0.64	-0.08	0.62
marbled murrelet	All states	0.57	<0.01	-0.24	0.35	-0.16	0.29
	California	0.59	<0.01	-0.48	0.05	-0.21	0.15
	Oregon	0.20	0.22	0.37	0.16	0.18	0.23
	Washington	0.27	0.05	0.02	1.00	-0.22	0.14
	Alaska	0.63	<0.01	0.09	0.76	0.10	0.50
double-crested cormorant	All states	-0.13	0.34	0.53	0.03	0.54	<0.01
	California	-0.27	0.05	0.09	0.76	0.53	<0.01
	Oregon	-0.02	0.89	0.46	0.06	0.21	0.16
	Washington	0.01	0.94	0.60	0.01	0.33	0.03
	Alaska	0.57	<0.01	0.46	0.06	-0.27	0.07
All species	All states	0.66	<0.01	-0.38	0.12	-0.04	0.78

3.3 Linear models

Linear models were conducted to examine what factors could best explain variations in population sizes of bird and fish species along the western coast of North America, from 1950 to 2012. The influence of the Pacific Decadal Oscillation index and sea surface temperature (through the HadISST dataset) on species populations were examined. The results of which linear models best explained variations in population size for each bird and fish species when all states were combined and in each state separately are displayed in tables and described below.

3.3.1 Fish species

Table 5 shows the results of which linear models best explained variations in the five species of Pacific salmon. When all the states used in this study were combined there were five different linear models that best explained population sizes, these were: fish competition, HadISST cycle removed, removal of all values of zero, HadISST trend removed and birds lagged by two years and fish by one year. The wide range of linear models that performed well for different species illustrates the breadth of variation within these populations and also between species of Pacific salmon. Table 5 shows that there was a similar situation when each state was considered separately and there was no obvious spatial pattern in which models performed the best for each salmon species. Notably, pink salmon had especially low adjusted R^2 values in California and Oregon, with linear models of birds and fish lagged by one year only able to account for less than 1% of total variation in commercial catch.

Table 5. Linear model results for the five species of Pacific salmon

Species	Location	Model	Model fit (adjusted R ²)
coho salmon	All states	fish competition	0.29
	California	birds 2 years and fish 1 year lag	0.54
	Oregon	removed 0 from the data	0.56
	Washington	HadISST trend removed	0.70
	Alaska	fish competition	0.63
sockeye salmon	All states	HadISST cycle removed	0.80
	Oregon	birds 2 years and fish 1 year lag	0.33
	Washington	birds 1 year lag	0.32
	Alaska	HadISST trend removed	0.73
chum salmon	All states	removed 0 from the data	0.60
	All states	HadISST trend removed	0.60
	Oregon	birds 2 years and fish 1 year lag	0.44
	Washington	birds 2 years and fish 1 year lag	0.48
	Alaska	HadISST trend removed	0.57
Chinook salmon	All states	fish competition	0.47
	California	birds 2 years and fish 1 year lag	0.31
	Oregon	HadISST cycle removed	0.46
	Washington	birds 2 years and fish 1 year lag	0.76
	Alaska	HadISST trend removed	0.43
pink salmon	All states	birds 2 years and fish 1 year lag	0.69
	California	birds and fish 1 year lag	0.06
	Oregon	birds and fish 1 year lag	0.07
	Washington	HadISST cycle removed	0.21
	Alaska	HadISST trend removed	0.68

Results of linear model runs on non-salmonid species are presented in table 6, which clearly shows that when all states were combined the best performing models were those involving sea surface temperature (SST) data from the HadISST dataset, with either the seasonal cycle or the long-term warming trend removed. For sardine and herring populations these models performed well, describing more than 45% of variation in populations. When the regional pattern across U.S. states was examined SST models performed less well. The linear model in which birds were lagged by two years and fish by one year, achieved R² values of greater than 0.50 for population sizes of herring in California and for sardine in Oregon. However, models of variations in zooplankton biomass in California were less successful (see table 6). HadISST averaged in California

with the cycle and trend removed could only account for 11% of total variation in this dataset.

Table 6. Linear model results for non-salmonid marine species

Species	Location	Model	Model fit (adjusted R ²)
sardine	All states	HadISST trend removed	0.61
	California	HadISST trend removed	0.68
	Oregon	birds 2 years and fish 1 year lag	0.57
	Washington	birds and fish 1 year lag	0.57
herring	All states	HadISST cycle removed	0.45
	All states	HadISST trend removed	0.45
	California	birds 2 years and fish 1 year lag	0.57
	Oregon	birds 2 years and fish 1 year lag	0.42
	Washington	removed 0 from the data	0.43
	Alaska	birds 2 years and fish 1 year lag	0.46
zooplankton	California	HadISST cycle removed	0.11
	California	HadISST trend removed	0.11

3.3.2 Bird species

Table 7 shows that variations in bird populations can be described by many different influencing factors. The linear models that best explained population sizes of common murre and marbled murrelet in all states included HadISST with the warming trend removed and birds lagged by one year, but these models accounted for less than 20% of the variation in the datasets. When divided into individual states, the models were improved and most were able to account for between 20% and 50% of the variations in bird populations in each state. Linear models that performed well for common murre and marbled murrelet in several states were birds lagged by one year, birds lagged by two years and fish by one year and HadISST with the long-term warming trend removed.

Results of linear models on double-crested cormorant populations were more positive, (see table 7) with all states except Alaska achieving over 65% of variation in the population explained. The linear model that best described double-crested cormorant population in all states had an R² value of 0.84, meaning that 84% of the variation in population size could be explained by HadISST data with the seasonal cycle removed.

Table 7. Linear model results for bird species

Species	Location	Model	Model fit (adjusted R ²)
common murre	All states	HadISST trend removed	0.13
	California	birds 1 year lag	0.33
	Oregon	birds 1 year lag	0.18
	Washington	birds 2 years and fish 1 year lag	0.25
	Alaska	HadISST cycle removed	0.39
	Alaska	HadISST trend removed	0.39
marbled murrelet	All states	birds 1 year lag	0.16
	California	birds 2 years and fish 1 year lag	0.30
	Oregon	birds 1 year lag	0.21
	Washington	birds 2 years and fish 1 year lag	0.21
	Alaska	HadISST trend removed	0.48
double-crested cormorant	All states	HadISST cycle removed	0.84
	California	HadISST cycle removed	0.68
	California	HadISST trend removed	0.68
	Oregon	birds 2 years and fish 1 year lag	0.73
	Washington	birds 2 years and fish 1 year lag	0.80
	Alaska	birds 1 year lag	0.16

4. Discussion

Before the results of this study can be interpreted, it is important to consider the degree to which there are 'events' in single years in the Pacific Decadal Oscillation index. There have been many year to year fluctuations in the PDO index over time (Mantua, 2002) and therefore there have often been PDO positive years within a negative or 'cool' phase and vice versa (Zwolinski and Demer, 2014). For this reason PDO phase shifts are sometimes said to be centred on a particular year (for example 1977). This variation can lead to identification of false shifts (Monastersky, 2000). For example, between 1958 and 1960 there was a temperature reversal in the PDO index that persisted for only two years before it returned to the previous conditions (Monastersky, 2000). In these circumstances, a period of hindsight of up to ten years is necessary to identify whether the PDO index has shifted into the opposite phase (Monastersky, 2000). Another cautionary note about interpretation of results presented in this study, is that strong correlations exist between events in the ocean and ecosystem responses, but this does not necessarily mean that ocean events are the primary cause of shifts in ecosystems (Woodward et al., 2008).

4.1 Interpretation of main results

4.1.1 Hypothesis 1- phase shifts of the Pacific Decadal Oscillation (PDO) index have influenced population sizes of fish and bird species in the Pacific Ocean ecosystem

The findings of this research clearly support this hypothesis that the PDO index has influenced population sizes in the North Pacific, at least to some extent. All species of fish together, (coho, Chinook, chum, sockeye and pink salmon and sardine and herring) in all states combined, showed a significant difference in population sizes before and after both the 1977 and 1989 shifts of the PDO index. When they were separated by species, all fish showed a response to the 1977 PDO phase change, apart from sardines. This result is particularly surprising because observations of changes in sardine populations were known before the climate drivers and sardines were instrumental in describing the pattern of Pacific Decadal Oscillation (Chavez et al., 2003). Therefore, of the all the fish species investigated as part of this study, sardines should have been

the most likely to show a response to changes in PDO phase. Other studies have found connections between sardine populations and the PDO index, especially in California where recruitment of sardines was found to increase after PDO positive years and decrease after PDO negative years (Zwolinski and Demer, 2014). One explanation for why commercial catch as an indicator of sardine populations in the Pacific Northwest does not appear to react to the 1977 PDO phase change is that sardines suffered a population crash along the coastline in the mid- 1950s (Emmett et al., 2005). Evidence suggests that populations took a long time to recover from this crash and sardines only commenced migrating to the west coast of North America in the mid-1990s (Emmett et al., 2005). Therefore, commercial catch of sardines remained extremely low in 1977 and did not show a regime shift because populations were still recovering.

Before and after 1989, all fish species showed a significant difference in population sizes, apart from herring and coho salmon. The records of commercial catch show that the majority of the herring population along the west coast of North America are caught in Alaska. This is significant because there is strong evidence to suggest that herring stock in Prince William Sound, Alaska collapsed in 1992 and were in steep decline before this time (Deriso et al., 2008). Deriso et al. (2008) found no correlations between the PDO phase change or the Exxon Valdez oil spill in 1989 and the onset of herring population decline. Therefore, although the herring stock collapse in Alaska was not caused by the Pacific Decadal Oscillation it does explain why commercial catch of herring showed no response to the 1989 shift. Deriso et al. (2008) also suggest that the practice of raising pink salmon in hatcheries in Alaska has contributed to the herring decline and subsequent lack of recovery, as juvenile pink salmon predate on and out compete juvenile herring.

Coho salmon also failed to show a response in population size to the 1989 event in the PDO index. The reasons for this are less clear cut than for herring populations, as coho salmon are not known to have experienced a major stock collapse in the area. A recent study has shown that there is little evidence from commercial catch of salmon in the North Pacific to support a shift in population sizes in 1989 (Irvine and Fukuwaka, 2011). However, the results of this study refute this conclusion, as four out of the five species of North Pacific salmon do

display a statistically significant difference in population size before and after 1989, suggesting that salmon stocks were part of an ecosystem regime shift at that point in time.

Populations of common murre, marbled murrelet and double-crested cormorant showed an altogether more varied response than the fish species to the two periods of the PDO studied. The findings suggest that common murre and marbled murrelet populations along the western coast of North America did not respond to either of the major regime shifts that were forced by the PDO in 1977 and 1989. This result appears to contradict evidence in the literature of studies which have shown that chick diet of murres is affected by the PDO index (Parrish and Zador, 2003), survival rates of marbled murrelets are related to the strength of the PDO index (Peery et al., 2006) and that there was a shift in the diet composition of marine birds that shows an ecosystem change in 1988 or 1989 (Sydeman et al., 2001). One reason that this study has not been able to replicate results of previous research into seabird populations is that the dataset of Christmas Bird Counts has weak sampling effort. This problem is further discussed in the limitations (section 4.2).

There are also a multitude of factors and other events that could be masking potential population responses of common murres and marbled murrelets to phase changes in the PDO index. These include population declines in Alaska due to the 1989 Exxon Valdez oil spill, which was estimated to have caused reductions of 10% of the murre population (Piatt and Anderson, 1996) and 3% of the marbled murrelet population (Carter and Kuletz, 1995) in the state. As previously discussed (in section 1.5.1), apex predators such as bald eagles and peregrine falcons also impact common murre populations in different ways (Paine et al., 1990; Parrish et al., 2001). Activities relating to the fishing industry are also complicating factors which can alter common murre and marbled murrelet population sizes, as commercial fishing reduces their prey resources and murres lose the option of prey switching (Ainley et al., 1996). Marbled murrelets are also forced to fish further down the food web and they have an increased importance of krill in their diet (Becker and Beissinger, 2006). One of the other major threats to seabird populations in the North Pacific is mortality from gill nets (Carter et al., 1995a). The cumulative effects of these factors and the 1982-83 ENSO event mean that populations of marbled murrelets have

been declining in Alaska since 1972 (Piatt and Naslund, 1995) and populations of common murre in California and Washington may have been in decline since 1980 and 1982 respectively (Piatt and Anderson, 1996). However, this is disputed with conflicting evidence proposing that populations of marbled murrelet in Washington and Oregon are not in long-term population decline (Varoujean II and Williams, 1995); this suggests that there is a spatial component to these population changes, with marbled murrelets in Alaska perhaps experiencing greater declines than elsewhere. Nevertheless, these declines and related conflicting factors could explain why no significant population change was detected in response to the 1977 or 1989 PDO events. However, double-crested cormorant populations did show a significant response to both North Pacific events, although for reasons discussed later (in section 4.1.2) changes in population size of this species are unlikely to be caused directly by the PDO index.

Another way that phase changes of the PDO index could have influenced populations of species, is in differences within and between 'cool' or negative PDO phases. As there were two negative PDO phases in the time period (1950-1977 and 1989-2012) of this study the population changes within each were compared. It was expected that each species would show a population difference between the two 'cool' PDO phases, because PDO as a single climatic index provides an incomplete picture of forcing across the North Pacific (Bond et al., 2003). It is therefore likely that although both were 'cool' PDO phases, each time period was subjected to slightly different conditions by other atmospheric and oceanic forcing factors (Bond et al., 2003). Indeed, as expected, all species of fish and double-crested cormorant in all states combined showed a significant population difference between the two 'cool' phases, apart from coho salmon. Whereas, common murre and marbled murrelet displayed no significant difference between these time periods, because as previously discussed they did not respond to any of the phase changes in the PDO index.

4.1.2 Hypothesis 2- 'warm' (positive) phases of PDO reduce productivity and population size of local fish and bird species

The second hypothesis related to the direction of change of zooplankton, fish and bird populations, by stating that 'warm' or positive phases of the Pacific Decadal Oscillation index would reduce productivity and therefore population sizes in the North Pacific ecosystem. This was expected because increases in ocean temperature have been linked to decreases in phytoplankton cell size, which can reduce production in the marine ecosystem (Gu enette et al., 2014). Furthermore, the California Current is weakened and contracted during the positive phase of the PDO, this results in decreased rates of upwelling and primary productivity in the area (Henderson et al., 2014). Previous studies have also found declines in populations that are more specifically associated with the 1977 PDO change to a positive phase. For instance, McGowan et al. (2003) concluded that this phase change was associated with biological population and biomass declines in the eastern North Pacific, or range shifts northwards for some species. These declines, starting in the late 1970s have been found across trophic levels in the Pacific marine ecosystem (McGowan et al., 2003). Seabird populations may have also been affected due to the decline of abundance of forage fish after 1977 (Francis et al., 1998).

The results of the Mann-Kendall tests for significant trends indicate that the PDO index did indeed display a positive phase, both over winter and annually for a decade between 1978 and 1988. Therefore, we would expect fish and bird species to show declines in this time period. It can be seen from the results of all states combined that the majority of fish species showed no significant trend after the 1977 phase shift in PDO index. Those species that did exhibit a significant trend were chum salmon and herring which were actually increasing in population size. This unexpected result for chum salmon may be due to the effect of combining all U.S.A. Pacific states together, as conditions from 1977 to 1989 particularly favoured stocks in Alaska and disfavoured stocks further down the coast (Hare et al., 1999). However, if this were true pink and sockeye salmon would also be expected to show this result, as they are the most productive salmon species in Alaskan fisheries (Hare et al., 1999). Therefore, why chum salmon and herring populations were increasing in the eastern North Pacific during the 'warm' PDO phase after 1977 needs further investigation.

By extending this hypothesis we might expect negative or 'cool' phases of the PDO index to result in increases in species population sizes, because ocean chlorophyll and therefore phytoplankton biomass has been shown to increase in 'cool' phases of the PDO index off California (Chavez et al., 2003). The annual PDO index was shown to have a negative trend after the shift in the Pacific in 1989, as was expected. The response of fish species to this event was very variable with three of the species showing a decrease, four showing no trend and two species showing the expected increase in population size. The species that increased were chum salmon and sardine. This result supports the findings of a study by Irvine and Fukuwaka (2011) which concluded that chum salmon increased in abundance after the 1989 shift. A study based in the Gulf of California also found that commercial catch of sardine increased by a massive 53% per year between 1969 and 1990 (Velarde et al., 1994), although this is likely due to recovery from the earlier sardine population collapse (Emmett et al., 2005; Tomczak and Godfrey, 1994).

The three species of fish that unexpectedly showed declining population trends in the 'cool' PDO phase after 1989 were coho salmon, Chinook salmon and herring. The population decline for herring at this time can be explained as the lead up to the collapse of stocks in Alaska in 1992 (Deriso et al., 2008). However, decreasing populations of coho and Chinook salmon are harder to explain. Indeed, this result contradicts previous studies that have found Chinook salmon productivity to be higher than expected in negative PDO phases in the North Pacific (Levin, 2003). The results obtained in this study could be the effect of adding together salmon populations across all Pacific U.S. states, this is because there is a large effect of latitude on abundance of salmon species and so populations in Alaska would be expected to decrease in negative PDO conditions, while further south along the coastline populations would be increasing (Drake et al., 2002). However, this does not satisfactorily explain why coho and Chinook salmon were the only species experiencing declines. Another potential explanation focuses on the life histories of these species, as coho and Chinook salmon juveniles rear in freshwater for extended periods before migrating to sea, compared to other species of salmon (Eggers et al., 2005). This could be a significant factor as the main climate influence on salmon populations is believed to occur early in their lifecycle (Eggers et al., 2005).

Therefore, coho and Chinook salmon are likely exposed to different climatic forcing factors whilst in freshwater rivers, when compared to other salmon species that are influenced by climate whilst in the Pacific Ocean. This differentiation between salmon species responses to climatic forcing factors needs further investigation.

There was a similar pattern of results for the three species of birds included in this study; only double-crested cormorant showed a significant population trend after 1989 and this was positive, as expected. However, there is considerable reason to believe that double-crested cormorant populations were not being forced predominately by natural or climatic factors for the duration of this study (1950-2012). Instead, there were significant anthropogenic actions that impacted directly and indirectly on population size of the species throughout North America, at this time. The most major of these anthropogenic impacts was contamination of the environment and subsequent poisoning from DDT and DDE, which historically reduced reproductive performance and population sizes of double-crested cormorant (U.S. Fish and Wildlife Service, 2005). Since DDT was banned in 1972 populations have been recovering (U.S. Fish and Wildlife Service, 2005) and reproductive performance of double-crested cormorants increased dramatically throughout the 1970s and 1980s (Sydeman et al., 2001). This population increase due to recovery from DDT poisoning has been amplified by a reduction in adult double-crested cormorant shootings, due to a ban in Oregon, also in 1972 (Carter et al., 1995b) and a subsequent reduction of human destruction of nests. All of these anthropogenic factors have meant that double-crested cormorant populations in North America were suppressed prior to 1972 and have subsequently displayed increases in populations that have not yet levelled off. Thus, this species cannot be considered to reliably reflect changes in population related to the phase of the PDO index.

4.1.3 Hypothesis 3- responses to phase shifts of the PDO index vary between the different trophic levels of zooplankton, fish and bird species in the Pacific Ocean ecosystem

Perhaps the most complex hypothesis of this study was that responses to phase changes of the PDO should vary between the different trophic levels of fish and bird species in the Pacific Ocean ecosystem. This variation in responses to the 1977 and 1989 phase shifts in the PDO index could manifest themselves in a threefold manner. Firstly as to whether population sizes show a response, then whether different increasing or decreasing trends occur over the same time period and finally whether there is a lag between the phase change and different population changes.

Overall, for the 1977 shift, the results showed that almost all species of fish and zooplankton responded with significant changes in population size. However, some bird species did not and common murre and marbled murrelet populations showed no significant response. The potential reasons for these results are discussed above. From these results it is possible to say that the three different trophic levels of zooplankton, fish and birds most likely displayed similar responses to the 1977 ecosystem regime shift, with some population changes occurring across all trophic levels at this time.

As regards to whether fish and bird species show contrasting population trends before and after the 1977 shift, when all species were combined fish showed a negative trend pre-1977 and no trend after 1977; zooplankton showed no significant trends at all and birds had a positive trend before 1977 and no trend after the phase change. From these results it can be concluded that there is a difference in population trends between different trophic levels in the North Pacific ecosystem, but only between 1950 and 1977. This result is interesting because the difference between population trends occurs before 1977 and there are no significant trends in any trophic level after this phase change in the PDO index. This result therefore supports the pattern seen in the line graphs of the PDO index in figure 11 and further reinforces the suggestion that the 1977 phase change began before this date and was potentially a ten year transition period, with the ecosystem of the North Pacific responding accordingly.

For the 1989 change in the phase of the PDO index, the majority of fish species showed a significant population response, as did zooplankton. However, similar to the pattern of events in 1977, both common murre and marbled murrelet showed no population response to the 1989 change of phase of the PDO index. When the results of all fish species, all bird species and zooplankton trends are analysed it is apparent that none of the species investigated in this study showed a significant increasing or decreasing population trend either before or after 1989. This result is significant because it supports the findings of a previous study on commercial catch of salmon in the North Pacific, which found little evidence to support a population shift after 1989 (Irvine and Fukuwaka, 2011). This finding can now be extended by the fact that none of the species included in this study displayed a significant increasing or decreasing population trend around 1989, but that some populations before and after this date are statistically significantly different from one another. Therefore, this study has found some evidence for an ecosystem regime shift in the North Pacific in 1989, but any changes at this time were not as major as they were in 1977. This is likely to be because in 1977 ENSO was strengthened because it was in phase with the PDO index; this seems to have caused more profound ecosystem shifts than the weaker PDO shift of 1989 which did not coincide with ENSO changes (Goodrich, 2004; Mantua, 2002; Woodward et al., 2008). The results of this study therefore support the theory that the 1989 event was not as influential on the North Pacific ecosystem as the 1977 event and that it was not just a simple reversal to the conditions established pre-1977 (Hare and Mantua, 2000).

Whether there were time lags between fish and bird species responses to the two PDO events in the North Pacific was investigated with linear models. Model numbers four, five, six, eight and nine were designed to incorporate the possible combinations of time lags between species and with the PDO index. Of these models, number six (birds lagged by two years and fish by one year without the PDO included) performed the best for both fish and bird species. This result suggests that there is some lag in interaction times between species, with birds responding to changes approximately one year behind fish species. Other studies have also found that changes at higher trophic levels in the North Pacific are out of phase with those at lower levels and this is a mechanism by which ecosystem regime shifts can eventually occur (Francis et al., 1998).

Responses to environmental stimuli are often more rapid at low trophic levels and this leads to a bottom-up effect on population control (Francis et al., 1998). Previous research has also shown that seabirds display lagged responses to both local (e.g. upwelling) and more distant (e.g. PDO) environmental changes (Ainley & Hyrenbach 2010). One study by Chapdelaine and Rail (1997) found the lag time between the highest catch of fish and the highest populations of herring gulls in Canada to be six years. This study shortens the lag time between changes in fish and bird populations to most likely one year, as linear models with greater than a two year lag performed badly, with low adjusted R^2 values. There is also another interesting finding in the literature which suggests that time lags can work the other way around when using commercial catch data for fish populations. Velarde et al. (1994) found that a reduction in seabird consumption of sardine preceded a reduction in the amount of sardine caught by three years. This is perhaps a result of birds being more sensitive to environmental conditions than the fishing industry, with birds changing their diet due to a decrease in fish populations before they are noticed by humans.

It is important to note that zooplankton appears to show no such time lag in relation to fish species. This result indicates that the lowest trophic level investigated in this study does not have a faster response to changes in the environment than fish species. Further studies need to be conducted in this area to ascertain whether this result is accurate.

4.1.4 Hypothesis 4- responses of species to PDO phase shifts vary latitudinally from north to south along the western coast of North America

The penultimate hypothesis in this study related to whether the responses of species to PDO phase shifts would vary latitudinally from north to south, along the western coast of North America. This was investigated by analysing the results for each USA Pacific state of Alaska, Oregon, Washington and California separately, as to whether they show population size responses to PDO phases, the direction of population trend and whether different factors are more or less important in each area.

The majority of fish species in most states displayed a significant difference in population sizes before and after 1977; the exceptions to this were in California with sardine and pink salmon and in Alaska with Chinook salmon. However, at

the 1989 shift results were not significant for a much greater range of species in different states: herring and coho salmon in Alaska, chum salmon in Washington, pink salmon in Oregon and Washington and zooplankton in California. Therefore, responses to environmental conditions were found to be not synchronous across all states on the western North American coastline, at either 1977 or 1989. This conclusion conflicts with evidence from a previous study that found simultaneous variations in sardine landings off California, Japan, Peru and Chile (Chavez et al., 2003).

Population trends of fish species in each state before and after both 1977 and 1989 were highly varied. For all species of Pacific salmon previous research has shown a highly spatial pattern of change along the west coast of North America (Drake et al., 2002). During positive PDO phases salmon stocks in Alaska experience high levels of abundance, whilst stocks further south in Oregon and California are in unfavourable conditions and therefore have declining populations (Drake et al., 2002). This is potentially because in 'warm' PDO phases salmon are displaced northward (Salinger, 2013). In the Columbia River, in Washington Chinook salmon stocks were relatively high during the negative PDO phase before 1977 but productivity was lower in the positive phase after 1977 (Levin, 2003). In addition, Hare et al. (1999) found that stocks of all salmon species between 1977 and 1989 were favoured in Alaska and disfavoured in Washington, Oregon and California. However, the results of this study initially appear to provide little evidence to support this research, as the 'warm' PDO phase between 1978 and 1988 resulted in no significant positive trends in Alaska. In 'cool' PDO phases southern salmon stocks in California and Oregon would be expected to be abundant and northern stocks in Alaska would be declining. The results of this study support this spatial pattern before 1977 for coho salmon and pink salmon, but no salmon species in the 'cool' PDO phase after 1989 conform to this pattern of spatial changes. This result ties in with the other findings in this study and builds on previous research which has found evidence for an ecosystem regime shift in 1989 to be sparse (Irvine and Fukuwaka, 2011).

For non-salmonid species spatial patterns were harder to investigate because data of commercial catch for sardines were only available in California. A previous study found that recruitment of sardine in California increases with

positive PDO conditions and decreases under negative conditions (Zwolinski and Demer, 2014). This study is unable to reproduce this pattern using commercial catch data of sardine in California. Herring show a spatial pattern similar to what was expected for the salmon species, with populations in Alaska decreasing during negative PDO conditions and increasing in positive ones. More southerly herring stocks in Oregon and Washington increased as expected in the negative PDO conditions before 1977. However, in the 'warm' phase after 1977 populations in Oregon continued to increase, while they decreased in Washington over the same time period. In addition, after 1989, herring populations in every state continued to decline. This continued decline in all states after 1989 may be as a result of other pressures on herring populations from commercial fishing and effects of climate change in the North east Pacific Ocean.

Zooplankton biomass showed no significant trends in California for any of the time periods between 1950 and 2012. This result was unexpected because previous research has found that macrozooplankton biomass has decreased by up to 80% between 1951 and 1993, this was likely due to the source of upwelling becoming shallower (Roemmich and McGowan, 1995). Indeed, it is well documented that the California Current System (CCS) is weakened under positive PDO conditions, which leads to decreased upwelling and productivity (Henderson et al., 2014), whilst in negative PDO phases the current is strengthened and becomes broader, thereby increasing primary productivity (Chavez et al., 2003). It is also well known that zooplankton (secondary productivity) is highly dependent on rates of primary production of phytoplankton and changes at the lowest level affect zooplankton abundance and distribution in the Pacific Ocean (Francis et al., 1998). Therefore, inferences about zooplankton populations can be made from chlorophyll concentrations in states other than California, this is significant because there is evidence that chlorophyll shows a latitudinal pattern with the Pacific Decadal Oscillation (Thomas et al., 2009). At high latitudes in the Pacific Ocean chlorophyll concentration is decreased during positive PDO phases (Thomas et al., 2009). However, another study found that zooplankton biomass does not follow this pattern so closely. Chavez et al. (2003) concluded that in warm PDO

phases zooplankton declined off the coasts of Oregon and Washington but increased off the higher latitude coast of Alaska.

Linear models for all fish species in every state individually were run to investigate whether there were spatial patterns involved in factors affecting population size. For the five species of Pacific salmon the best performing linear model in each state varied widely with the only consistent pattern being the model with HadISST trend removed, which explained most variation in populations in Alaska in all species, except for coho salmon. The results for linear models of non-salmonid species were equally variable with no distinctive spatial pattern emerging.

For the three species of seabird investigated in this study, common murre and double-crested cormorants showed significant population differences before and after the 1977 PDO event in all states and marbled murrelets had significant differences in all states apart from Washington. This supports previous evidence which suggests that 1977 was a major phase change with populations in nearly all states showing a response. At the 1989 phase change in the PDO index, common murre showed a population response in only California and Washington, marbled murrelets displayed a significant difference in Washington and Alaska, whilst double-crested cormorant populations were significantly different in all states at this time.

In general, bird population trends were expected to show declines during positive PDO conditions and increases in negative phases along the western coast of North America (Vandenbosch, 2000). The results of this study support this finding to some extent as populations of seabird species in most states increased in the negative PDO phase before 1977. However, only marbled murrelet in California displayed a decreasing population in the 'warm' phase after 1977, this pattern was expected from other seabird populations based on a study by Chavez et al. (2003). In addition, after 1977 range shifts northwards were observed for some species (McGowan et al., 2003), this study did not detect increasing populations of seabird species at northerly latitudes under positive PDO conditions. During the second negative PDO phase investigated in this study, after 1989, the majority of species in each state showed no significant population trends. This supports evidence from a previous study in British Columbia which found marbled murrelet counts from the Christmas Bird

Count dataset show no clear trends between 1957 and 1992 (Rodway et al., 1992). However, in California these results were somewhat unexpected as previous research has indicated seabird abundance in the area declined by approximately 40% between 1987 and 1994 (Veit et al., 1996). Common murre populations in Washington at this time decreased, this may be as a result of increasing apex predator effects reducing population size by 3% per year (Parrish et al., 2001). Double-crested cormorants after 1989 showed the expected increase in populations due to negative PDO conditions, but only in California and Washington and as previously discussed these population changes have been profoundly influenced by factors other than Pacific Decadal Oscillation.

Linear models were also run on species of seabird to identify whether there are any common variables influencing population sizes in specific states. Similar to the fish species, the results were highly variable but it is possible to pick out some spatial patterns. The model that was best at explaining variation in common murre and marbled murrelet populations in Oregon was birds lagged by one year, whilst the model with birds lagged by two years and fish by one year explained most variation in all three species in Washington and the model of HadISST with warming trend removed performed well for common murre and marbled murrelet in Alaska.

4.1.5 Hypothesis 5- sea surface temperature (SST) data from the HadISST dataset will explain less variation in populations of fish and bird species than the PDO index

The fifth and final hypothesis of this study was that sea surface temperature (SST) data from the HadISST dataset would explain less variation in fish and bird populations than the PDO index. This was hypothesised because the PDO index represents the spatial pattern of SST anomalies across the Pacific Ocean and it has a basin-wide effect on abundance of species, whereas individual SST anomalies would be expected to have a more localised influence (Litzow and Mueter, 2014). The difference between these two climate indices was highlighted in a recent study that found over the last century in the North Pacific, sea surface temperatures have shown PDO variations in addition to a warming trend of between 0.5 °C and 1 °C (Johnstone and Mantua, 2014). One of the reasons a difference in species response between HadISST and PDO index

was expected is because the PDO index does not include this recent warming trend (Johnstone and Mantua, 2014). In addition, increasing SSTs produce a more spatially uniform warming pattern than the PDO does (Overland and Wang, 2007) and SST variations over decadal timescales in the North Pacific do not display abrupt transitions (Masuda, 2002).

The results of the linear model runs clearly show that models which involved the HadISST dataset with the seasonal cycle removed and the long-term warming trend removed (similar to the PDO index) were successful at explaining population variations in most fish species. These two models best explained populations of sockeye salmon, chum salmon, sardine and herring when SSTs from the HadISST dataset were averaged over all states. In particular, in Alaska HadISST data with the long-term warming trend removed was successful in accounting for up to 73% of variation in populations of four out of the five species of Pacific salmon.

When these results of linear models with HadISST data are compared to those with the PDO index included (model numbers 7, 8 and 9) it becomes apparent that none of the population sizes of species of fish either in all states combined, or in each area separately can be satisfactorily accounted for by the PDO index. This stark result disproves the hypothesis in question and leads us to conclude that the more localised SST anomalies have a greater influence on population sizes of fish in the North Pacific than the basin-wide pattern of the PDO index. In addition, the HadISST model with the long-term warming trend removed generally performed better for species of fish and birds than the model with seasonal cycle removed. This suggests that the majority of fluctuation in population size is due to climate variability and not the influence of anthropogenic climate change.

The two best models that were capable of explaining some variation in zooplankton biomass in California involved the HadISST dataset and whilst they could only account for 11% of this variation they still performed better than those linear models involving the PDO index. This result indicates that more localised SST anomalies in California influence zooplankton biomass more than the basin-wide PDO pattern of anomalies. This result therefore supports the findings of a recent study that found ocean water temperatures are closely related to the concentration of nitrate in upwelling regions, which in turn controls

plankton productivity (García-Reyes et al., 2014). In addition, another recent study that expands on the findings of the research presented here, suggests that in the California Current changes in the sign of the PDO index are more influential on variations of plankton community structure than seasonally averaged upwelling (Du et al., 2015). The authors of this paper suggest this result is due to changes in the strength of the current associated with phase changes of the PDO index (Du et al., 2015). Therefore, when combined with the results of this study, zooplankton populations may be more influenced by local SST measurements than the PDO index in terms of abundance, but more influenced by PDO phases than upwelling in terms of community structure and the mix of zooplankton species present.

For the three species of seabird in this study the two models involving HadISST data were best at explaining population variations across all states for common murre and double-crested cormorant, whereas marbled murrelet abundance could be better accounted for by simply lagging them one year behind fish populations. When each state was considered separately, as with the fish species, the linear model with HadISST warming trend removed best explained variation in Alaska for common murre and marbled murrelet. However, both HadISST seasonal cycle removed and warming trend removed accounted for the most population variation of double-crested cormorant in California. Moreover, as for the results for fish species, linear models including the PDO index could not account for the most variability in seabird populations either when all regions were averaged or in each state separately. This once more disproves the hypothesis that PDO index would have a greater influence on populations than SST anomalies from HadISST.

A possible explanation for this finding is that this study examines timeseries of fish, zooplankton and seabirds from only one area of the PDO index. This means that at any one time the other sign of the PDO index is unaccounted for in the linear models presented here. Another plausible explanation that requires further study is that an individual timeseries of abundance of a population at a single location along the coast of North America would be influenced by local changes in sea surface temperatures, more than regional basin-wide changes. However, this reasoning does not account for why when populations in each

state were combined, they also showed greater correlations with HadISST than the PDO index.

4.2 Limitations

The limitations of commercial catch of fish species are well documented on the NOAA Office of Science and Technology website (NOAA, 2015b). In the context of this study the most relevant limitation of this dataset and something that cannot be mitigated for, is that due to confidentiality laws data on some specific species landings may be incomplete and therefore misleading (NOAA, 2015b). In addition, there is a complication with the spatial element of the data as commercial landings indicate the state in which the fish crossed the dock and not necessarily the state in which the fish were caught (NOAA, 2015b).

Therefore, this research has potential errors by assuming that the individual data from each state reflect where the fish were caught. Additionally, there is a limitation of lack of independence in this timeseries, because catch in one year is likely to be influenced by catch in the previous year (Irvine and Fukuwaka, 2011). Commercial catch rates of fish are generally accepted to be indicative of abundance, at least to a first order approximation (Hare et al., 1999). However, some argue that the use of catch data as a proxy for population abundance is only valid when anthropogenic exploitation rates and management practices remain constant over time (Eggers et al., 2005). Clearly from 1950 to 2012, both of these factors have changed in the North Pacific. Therefore, catch rates used in this study may not be absolute proxies for abundance of fish species, but they are still considered to be good approximations and many studies have used this data. This is because commercial catch is often the longest and most consistent record of fish populations available (Irvine and Fukuwaka, 2011).

Data caveats on zooplankton biomass from California Cooperative Oceanic Fisheries Investigations (CalCOFI) are quite limited, with the only important thing to note being that data collection methods have changed over the time period investigated in this study. In 1978 the diameter of the sampling net used was decreased from a 1 meter ring net to a 0.71 meter bongo net (Ohman and Smith, 1995). This change improved collection of motile zooplankton and generally resulted in a significant change in recorded zooplankton biomass in 1978 (Ohman and Smith, 1995). Due to the timing, this change is particularly important because it could have interfered with the results of significant shifts in

zooplankton biomass with the PDO phase change in 1977, potentially causing false positive results.

For data from the Christmas Bird Count (CBC) there are some important limitations that may influence the results of this study. First of all, this study relies on data of seabird species and the Christmas Bird Count is not done offshore, therefore some populations of each species are likely to be missed due to the data collection methods used. In addition, there is a very short count period of between 14th December and 5th January (National Audubon Society, 2015), which in this study is taken as a proxy for bird species abundance for the whole year. To minimise the effects of this limitation on the results of this study only bird species that are resident on the west coast of North America year-round were included, thus eliminating the effects of migrating populations.

Finding an appropriate proxy of seabird abundance is a difficult task. Catch rates of seabirds as bycatch in fishing nets is known to reflect availability of prey but not absolute population abundance (Cairns, 1992). In addition, seabirds can only reflect fish abundance up to a threshold, because beyond this point a factor other than food supply will limit population size (Monaghan, 1996). In the context of this study, these limitations are important because they indicate that the data of seabird counts used in this research are appropriate proxies of population size, but also that inferences about fish populations drawn from this data may not be valid. Therefore, this study has avoided making such inferences, to minimise the potential limitations of using this data.

For data of climate indices (PDO index and HadISST) there are some limitations associated with the way in which they are compiled or calculated. There is some uncertainty in the PDO index after the late 1990s due to the choice of SST dataset and EOF vector used when calculating the PDO index (Wen et al., 2014). However, this uncertainty is most apparent when the PDO index from different centres are compared (Wen et al., 2014) and because this study took the index from only one source, it is considered to have a negligible effect on the results of this research. Additionally, it is known that there is a high risk of encountering false-positive results when working with red spectral timeseries such as the PDO climate index (Di Lorenzo and Ohman, 2013; Harrison and Chiodi, 2014). Studies have shown that this risk is present even with a careful statistical approach (Harrison and Chiodi, 2014) and therefore the

results of PDO index analysis within this study should be used with some caution. The HadISST dataset from the Met Office Hadley Centre contains data on both SSTs and sea ice extent and concentration from 1870 to present (Met Office, 2015). However, there is a discontinuity in this record of sea ice in January 2009 due to a change in the data source; this change also affected the sea surface temperature record because sea ice is used to calculate SST in some areas (Met Office, 2015).

In addition, the statistical significance of a historical trend is not an appropriate base for speculation about the future (Harrison and Chiodi, 2014) and as such, this study is not intended to be used for this purpose.

5. Conclusion

To summarise, this study has found that the phase change of the Pacific Decadal Oscillation index which started in the early 1970s and continued for approximately ten years did coincide with a major ecosystem regime shift in the North Pacific, with the three trophic levels of zooplankton, fish and birds responding differently to this event. In addition, there is some evidence to support another ecosystem regime shift occurred in 1989, associated with a change in PDO phase. Consistent with conclusions of other studies, the shift at this time was found to be less pronounced than in 1977 (Benson and Trites, 2002). Furthermore, ecological responses were generally not synchronous along the west coast of North America, either after 1977 or after 1989, with salmon species showing an especially strong spatial pattern. Perhaps the most unexpected result of this study is that sea surface temperature (SST) anomalies from the HadISST dataset, especially with the long-term global warming trend removed, explain variations in population sizes of fish and bird species and biomass of zooplankton better than the PDO index. This result indicates that localised SSTs may have a greater influence on population sizes in the North Pacific than the basin-wide PDO index.

This work contributes to our understanding of marine ecosystem responses to climatic events and changing sea surface temperatures. These results are important because they extend the knowledge of the research area by comparing responses of species at different trophic levels to the PDO index, across all U.S.A. Pacific states.

To advance study in this area in the future, it is suggested that further research should focus on investigating whether and attempting to explain why, localised SST anomalies may influence abundance of various species in the North Pacific more than the PDO index. In addition, research should be conducted to further our understanding of trends in zooplankton populations in relation to the PDO index, across all U.S. Pacific states. This research could be conducted using zooplankton size instead of biomass as an indicator of changing temperatures, trophic links and feeding strategy (Chiba et al., 2015). Furthermore, studies into the generation time of fish and bird species in the North Pacific could be conducted to account for variations in abundance over the whole life history (Hsieh and Ohman, 2006). Such a study would be useful to ascertain whether

populations passively track environmental variables or whether they are amplifications of physical forcing.

Appendix 1: R codes

Data processing

Climate indices

PDO index divided into annual and winter

```
pdo <- read.table('pdo_ts_240914.txt')
```

```
pdoyear <- pdo[,1]
```

```
pdoyear
```

```
pdo <- pdo[,2]
```

```
annual_pdo <- rep(NA, 112)
```

```
for (i in 1:112) {annual_pdo[i] <- mean(pdo[((i-1)*12+1):(i*12)])}
```

```
annual_pdo
```

```
annual <- annual_pdo[50:112]
```

```
decembers <- seq(12,112*12,by=12)
```

```
jan <- seq(1,112*12,by=12)
```

```
feb <- seq(2,112*12,by=12)
```

```
winters <- union(decembers,jan)
```

```
winters <- union(winters,feb)
```

```
winters <- sort(winters)
```

```
importantwinter <- winters[147:335] #goes from dec 1949 to feb 2012
```

```
importantpdo <- pdo[importantwinter]
```

```
winter_pdo <- rep(NA, 63)
```

```
for (i in 1:63) {winter_pdo[i] <- mean(importantpdo[((i-1)*3+1):(i*3)])}
```

```
winter <- winter_pdo
```

E.g. California HadISST cycle and trend removed

```
cali_ts <- rep(NA, 1699)
```

```
for (i in 1:1699) {
```

```
    temparray <- as.matrix(california[,i])
```

```
    tempvec <- as.vector(temparray)
```

```
    cali_ts[i] <- mean(na.omit(tempvec))
```

```
}
```

```
cali_ts <- cali_ts/100
```

```

pre11 <- cali_ts[1:1692]
cyclemat <- matrix(pre11, ncol=12, byrow=TRUE)
meancycle <- rep(NA, 12)
for (i in 1:12) {
    meancycle[i] <- mean(cyclemat[,i])
}
cycles <- rep(meancycle, 141)
cycles <- c(cycles, meancycle[1:7])
plot(year,cali_ts,type="l", main='North Pacific SST California Subregion',
xlab='Year', ylab='Average SST (C)')
lines(year,cycles,col='red')
decycle <- cali_ts - cycles
model <- lm(decycle ~ year + I(year^2))
trend <- model$coefficient[3]*year^2 + model$coefficient[2]*year +
model$coefficient[1]
plot(year,decycle,type="l", main='North Pacific SST 20-60N California
Subregion Decycled', xlab='Year', ylab='Anomaly From Mean SST')
lines(year,trend,col='red')
detrend <- decycle - trend

```

Statistical analyses

Investigating distribution of the data

E.g. marbled murrelet

```
shapiro.test(murrelet$California)
```

```
shapiro.test(murrelet$Oregon)
```

```
shapiro.test(murrelet$Washington)
```

```
shapiro.test(murrelet$Alaska)
```

```
hist(log(murrelet$California),main=NULL,xlab="Marbled murrelet (per party
hour) in California")
```

```
hist(log(murrelet$Oregon),main=NULL,xlab="Marbled murrelet (per party hour)
in Oregon")
```

```
hist(log(murrelet$Washington),main=NULL,xlab="Marbled murrelet (per party
hour) in Washington")
```

```
hist(log(murrelet$Alaska),main=NULL,xlab="Marbled murrelet (per party hour)
in Alaska")
```

Wilcoxon rank sum tests

E.g. marbled murrelet

```
wilcox.test(murrelet$California[31:58],murrelet$California[59:95])
```

```
wilcox.test(murrelet$Oregon[31:58],murrelet$Oregon[59:95])
```

```
wilcox.test(murrelet$Washington[31:58],murrelet$Washington[59:95])
```

```
wilcox.test(murrelet$Alaska[31:58],murrelet$Alaska[59:95])
```

```
wilcox.test(murrelet$California[59:69],murrelet$California[70:95])
```

```
wilcox.test(murrelet$Oregon[59:69],murrelet$Oregon[70:95])
```

```
wilcox.test(murrelet$Washington[59:69],murrelet$Washington[70:95])
```

```
wilcox.test(murrelet$Alaska[59:69],murrelet$Alaska[70:95])
```

```
murrelet$California[which(is.na(murrelet$California)==TRUE)] <- 0
```

```
murrelet$Oregon[which(is.na(murrelet$Oregon)==TRUE)] <- 0
```

```
murrelet$Washington[which(is.na(murrelet$Washington)==TRUE)] <- 0
```

```
murrelet$British_Columbia[which(is.na(murrelet$British_Columbia)==TRUE)] <- 0
```

```
murrelet$Alaska[which(is.na(murrelet$Alaska)==TRUE)] <- 0
```

```
murrelet$all<-
```

```
murrelet$California+murrelet$Oregon+murrelet$Washington+murrelet$British_Columbia+murrelet$Alaska
```

```
wilcox.test(murrelet$all[31:58],murrelet$all[59:95])
```

```
wilcox.test(murrelet$all[59:69],murrelet$all[70:95])
```

E.g. marbled murrelet comparison between 'warm' and 'cool' PDO phases

```
wilcox.test(murrelet$California[c(31:58,70:95)],murrelet$California[59:69])
```

```
wilcox.test(murrelet$Oregon[c(31:58,70:95)],murrelet$Oregon[59:69])
```

```
wilcox.test(murrelet$Washington[c(31:58,70:95)],murrelet$Washington[59:69])
```

```
wilcox.test(murrelet$Alaska[c(31:58,70:95)],murrelet$Alaska[59:69])
```

```
wilcox.test(murrelet$all[c(31:58,70:95)],murrelet$all[59:69])
```

PDO index

```
wilcox.test(annual[c(1:27)],annual[c(28:63)])
```

```
wilcox.test(annual[c(28:38)],annual[c(39:63)])
```

```
wilcox.test(winter[c(1:27)],winter[c(28:63)])
```

```
wilcox.test(winter[c(28:38)],winter[c(39:63)])
```

```
wilcox.test(annual[c(1:27,39:63)],annual[c(28:38)])
```

```
wilcox.test(winter[c(1:27,39:63)],winter[c(28:38)])
```

```
wilcox.test(annual[c(1:27)],annual[c(39:63)])
```

```
wilcox.test(winter[c(1:27)],winter[c(39:63)])
```

Mann-Kendall tests

E.g. marbled murrelet

```
library(Kendall)
```

```
murrelet1<-MannKendall(murreletall[1:28])
```

```
murrelet2<-MannKendall(murreletall[29:39])
```

```
murrelet3<-MannKendall(murreletall[40:63])
```

```
murreletcali1<-MannKendall(murreletcalifornia[1:28])
```

```
murreletcali2<-MannKendall(murreletcalifornia[29:39])
```

```
murreletcali3<-MannKendall(murreletcalifornia[40:63])
```

```
murreletor1<-MannKendall(murreletoregon[1:28])
```

```
murreletor2<-MannKendall(murreletoregon[29:39])
```

```
murreletor3<-MannKendall(murreletoregon[40:63])
```

```
murreletwash1<-MannKendall(murreletwashington[1:28])
```

```
murreletwash2<-MannKendall(murreletwashington[29:39])
```

```
murreletwash3<-MannKendall(murreletwashington[40:63])
```

```
murreletal1<-MannKendall(murreletalaska[1:28])
```

```
murreletal2<-MannKendall(murreletalaska[29:39])
```

```
murreletal3<-MannKendall(murreletalaska[40:63])
```

Climate indices

```
winter1<-MannKendall(winter[1:28])
```

```
winter2<-MannKendall(winter[29:39])
```

```
winter3<-MannKendall(winter[40:63])
```

```
annual1<-MannKendall(annual[1:28])
```

```
annual2<-MannKendall(annual[29:39])
```

```
annual3<-MannKendall(annual[40:63])
```

```
HADISST1<-MannKendall(annual[1:28])
```

```
HADISST2<-MannKendall(annual[29:39])
```

```
HADISST3<-MannKendall(annual[40:63])
```

```
HADISST1<-MannKendall(decycle_cut[1:28])
HADISST2<-MannKendall(decycle_cut[29:39])
HADISST3<-MannKendall(decycle_cut[40:63])
HADISST1<-MannKendall(detrend_cut[1:28])
HADISST2<-MannKendall(detrend_cut[29:39])
HADISST3<-MannKendall(detrend_cut[40:63])
```

Linear models

E.g. marbled murrelet

```
mod2<-
lm(murreletall~herringall+chumall+cohoall+sockeyeall+chinookall+pinkall+sardinesall)
```

```
summary(mod2)
```

```
mod2<-
lm(murreletcalifornia~herringcalifornia+cohocalifornia+chinookcalifornia+pinkcalifornia+sardinescalifornia+zoocalifornia+annual+winter)
```

```
summary(mod2)
```

```
modoregon<-
lm(murreletoregon~herringoregon+cohooregon+chinookoregon+pinkoregon+sardinesoregon+annual+winter)
```

```
summary(modoregon)
```

```
modwashington<-
lm(murreletwashington~herringwashington+chumwashington+cohowashington+sockeyewashington+chinookwashington+pinkwashington+sardineswashington+annual+winter)
```

```
summary(modwashington)
```

```
modalaska<-
lm(murreletalaska~herringalaska+chumalaska+cohoalaska+sockeyealaska+chinookalaska+pinkalaska+annual+winter)
```

```
summary(modalaska)
```

Effects of competition

```
mod2<-lm(murreletall~murreall+cormorantall+annual+winter)
```

```
summary(mod2)
```

Including PDO index

```
murrelet<-lm(murreletall~
herringall+chumall+cohoall+sockeyeall+chinookall+pinkall+sardinesall+zooall+annual+winter)
```

summary (murrelet)

Removing values of zero

```
murreletall<-murreletall[c(3,4,7:19,22,24,25,27:63)]
```

```
murrelet<-lm(murreletall~  
herringall+chumall+cohoall+sockeyeall+chinookall+pinkall+sardinesall+zooall+a  
nnual+winter)
```

summary (murrelet)

Birds lagged by one year

```
murrelet$all_shift<-c(NA,murrelet$all[1:94])
```

```
murreletshift<-murrelet$all_shift[31:93]
```

```
murreletlag<-  
lm(murreletshift~herringall+chumall+cohoall+sockeyeall+chinookall+pinkall+sar  
dinesall)
```

summary(murreletlag)

```
murrelet$cali_shift<-c(NA,murrelet$California[1:94])
```

```
murreletcali<-murrelet$cali_shift[31:93]
```

```
murrelet$or_shift<-c(NA,murrelet$Oregon[1:94])
```

```
murreletor<-murrelet$or_shift[31:93]
```

```
murrelet$wash_shift<-c(NA,murrelet$Washington[1:94])
```

```
murreletwash<-murrelet$wash_shift[31:93]
```

```
murrelet$al_shift<-c(NA,murrelet$Alaska[1:94])
```

```
murreletal<-murrelet$al_shift[31:93]
```

mod2<-

```
lm(murreletcali~herringcalifornia+cohocalifornia+chinookcalifornia+pinkcaliforni  
a+sardinescalifornia+zooalifornia+annual+winter)
```

summary(mod2)

modoregon<-

```
lm(murreletor~herringoregon+cohooregon+chinookoregon+pinkoregon+sardine  
soregon+annual+winter)
```

summary(modoregon)

modwashington<-

```
lm(murreletwash~herringwashington+chumwashington+cohowashington+socke  
yewashington+chinookwashington+pinkwashington+sardineswashington+annu  
al+winter)
```

summary(modwashington)

```
modalaska<-  
lm(murrelet~herringalaska+chumalaska+cohoalaska+sockeyealaska+chinook  
alaska+pinkalaska+annual+winter)
```

```
summary(modalaska)
```

Birds lagged by two years

```
murreshift<-murre$all[4:64]
```

```
murreletshift<-murrelet$all[33:93]
```

```
cormorantshift<-cormorant$all[18:78]
```

```
herringshift<-herring$all[3:63]
```

```
chumshift<-chum$all[3:63]
```

```
cohoshift<-coho$all[3:63]
```

```
sockeyeshift<-sockeye$all[3:63]
```

```
chinookshift<-chinook$all[3:63]
```

```
pinkshift<-pink$all[3:63]
```

```
sardinesshift<-sardines$all[3:63]
```

```
zooshift<-zoo$zooplankton[3:63]
```

```
annual<-annual[1:61]
```

```
winter<-winter[1:61]
```

```
mod2<-
```

```
lm(murreletshift~herringshift+chumshift+cohoshift+sockeyeshift+chinookshift+pi  
nkshift+sardinesshift+zooshift+annual+winter)
```

```
summary(mod2)
```

HadISST seasonal cycle removed

```
murreletcalifornia<-murrelet$California[31:91]
```

```
murreletoregon<-murrelet$Oregon[31:91]
```

```
murreletwashington<-murrelet$Washington[31:91]
```

```
murreletalaska<-murrelet$Alaska[31:91]
```

E.g Oregon

```
mod1<-
```

```
lm(murreletoregon~murreoregon+cormorantoregon+herringoregon+cohooregon  
+chinookoregon+pinkoregon+sardinesoregon+sockeyeoregon+chumoregon+or  
egon)
```

```
summary(mod1)
```

HadISST warming trend removed

E.g. Oregon

```
oregonde <- detrend[961:1692]
oregondetrend <- rep(NA, 61)
for (i in 1:61) {oregondetrend[i] <- mean(oregonde[((i-1)*12+1):(i*12)])}
oregondetrend
mod1<-
lm(murreletoregon~murreoregon+cormorantoregon+herringoregon+cohooregon
+chinookoregon+pinkoregon+sardinesoregon+sockeyeoregon+chumoregon+oregondetrend)
summary(mod1)
```

Figures

Figure 2. Illustration of the difference between white and red noise

```
white <- 0.05*rnorm(1000)
red <- rep(NA, 1000)
red[1] <- white[1]
for (i in 2:1000) {red[i] <- 0.95*red[i-1] + white[i]}
spec_white <- spectrum(white)
spec_red <- spectrum(red)
layout(matrix(c(1,2,3,4), byrow=T, ncol=2), widths=c(4,3))
plot(white, type="l", xlab="", ylab="White noise",ylim=range(red))
plot(spec_white$freq, log(spec_white$spec), type="l", xlab='Frequency',
ylab='Spectrum', ylim=range(log(spec_red$spec)))
plot(red, type="l", xlab="",ylab="Red noise")
plot(spec_red$freq, log(spec_red$spec), type="l", xlab='Frequency',
ylab='Spectrum')
```

Figure 8. Map of the Pacific region showing SST data from the HadISST dataset

```
library(maps)
library(mapdata)
library(mapproj)
load('HadISST_PDO_data_20_60_0812.RData')
source('plotmap2.R')
plotmap2 = function(lon, lat, data, breaks, title = "") {
  ncol = length(breaks) - 1
```

```

cbar = heat.colors(ncol)
coast = map("world2", interior = FALSE, plot = FALSE)
layout(matrix(1:2), heights = c(5, 1))
par(mar=c(5,3,0.2,3))
image(lon, lat, data, col = rev(cbar), axes =
TRUE,xlab='Longitude',ylab='Latitude', breaks = breaks)
map(coast, add = TRUE)
lines(c(233,240),c(34,34))
lines(c(240,240),c(34,42))
lines(c(233,240),c(42,42))
lines(c(233,233),c(42,34))
lines(c(231,236),c(42,42))
lines(c(236,236),c(42,46))
lines(c(231,236),c(46,46))
lines(c(231,231),c(42,46))
lines(c(231,236),c(46,46))
lines(c(236,236),c(46,48))
lines(c(231,236),c(48,48))
lines(c(231,231),c(46,48))
lines(c(190,220),c(50,50))
lines(c(220,220),c(50,60))
lines(c(190,220),c(60,60))
lines(c(190,190),c(50,60))
box()
par(mar = c(3, 0.5, 0.1, 0.5), mgp = c(1.3, 0.3, 0), las = 1)
image(1:ncol, 1, matrix(1:ncol), col = rev(cbar), axes = FALSE, xlab = title, ylab
= "")
axis(1, at = 0:ncol+0.5, labels = breaks, tick = FALSE)
box()
}
plotmap2(lon+180,lat,spatarray[,961]/100, seq(-5,30,by=5), 'HadISST January
1950')

```

Figure 11. Graphs of climate indices used in this study

```
par(mfrow=c(2,2))
plot(year2$Year,annual,type="l",xlab="Year",ylab="Annual PDO index",ylim=c(-2,2))
plot(year2$Year,winter,type="l",xlab="Year",ylab="Winter PDO index")
abline(v=1977,col="red",lty=2)
abline(v=1989,col="red",lty=2)
mtext("(a)", side = 3, line = -4, adj = 0.1, cex = 1,outer=TRUE)
mtext("(b)", side = 3, line = -4, adj = 0.6, cex = 1,outer=TRUE)
mtext("(c)", side = 3, line = -23, adj = 0.1, cex = 1,outer=TRUE)
mtext("(d)", side = 3, line = -23, adj = 0.6, cex = 1,outer=TRUE)
plot(annualyear,decycle_cut,type="l", main='North Pacific SST 20-60N
Decycled', xlab='Year', ylab='Anomaly From Mean SST')
plot(year_year,cali,type="l",col="blue",xlab="Year",ylab="HADISST (anomaly
from mean °C)",ylim=c(-1,2))
lines(year_year,or,col="green")
lines(year_year,washi,col="hotpink")
lines(year_year,ala,col="orange")
lines(annualyear,decycle_cut)
plot(year_year,calidetrend,type="l",col="blue",xlab="Year",ylab="HADISST
(anomaly from mean °C)",ylim=c(-1,1.5))
lines(year_year,oregondetrend,col="green")
lines(year_year,washdetrend,col="hotpink")
lines(year_year,alaskadetrend,col="orange")
lines(annualyear,totaldetrend)
```

Figure 12. Box and whisker plots showing quantities of coho salmon (a), sockeye salmon (b), chum salmon (c), Chinook salmon (d) and pink salmon (e) caught in all states over three time periods

```
par(mfrow=c(3,2))
boxplot(coho$all[1:28],coho$all[29:39],coho$all[40:63],names=c('1950-1977','1978-1988','1989-2012'),xlab="Year",ylab="coho salmon (metric tons caught)")
boxplot(sockeye$all[1:28],sockeye$all[29:39],sockeye$all[40:63],names=c('1950-1977','1978-1988','1989-2012'),xlab="Year",ylab="sockeye salmon (metric tons caught)")
```

```
boxplot(chum$all[1:28],chum$all[29:39],chum$all[40:63],names=c('1950-1977','1978-1988','1989-2012'),xlab="Year",ylab="chum salmon (metric tons caught)")
```

```
boxplot(chinook$all[1:28],chinook$all[29:39],chinook$all[40:63],names=c('1950-1977','1978-1988','1989-2012'),xlab="Year",ylab="chinook salmon (metric tons caught)")
```

```
boxplot(pink$all[1:28],pink$all[29:39],pink$all[40:63],names=c('1950-1977','1978-1988','1989-2012'),xlab="Year",ylab="pink salmon (metric tons caught)")
```

Figure 13. Box and whisker plots showing quantities of sardine (a) and herring (b) caught in all states, all fish species in all states combined (c) and zooplankton biomass in California (d) over three time periods

```
par(mfrow=c(2,2))
```

```
boxplot(sardines$all[1:28],sardines$all[29:39],sardines$all[40:63],names=c('1950-1977','1978-1988','1989-2012'),xlab="Year",ylab="sardines (metric tons caught)")
```

```
boxplot(herring$all[1:28],herring$all[29:39],herring$all[40:63],names=c('1950-1977','1978-1988','1989-2012'),xlab="Year",ylab="herring (metric tons caught)")
```

```
boxplot(totalfish[1:28],totalfish[29:39],totalfish[40:63],names=c('1950-1977','1978-1988','1989-2012'),xlab="Year",ylab="All fish species (metric tons caught)")
```

```
boxplot(zoo$zooplankton[1:27],zoo$zooplankton[28:38],zoo$zooplankton[39:63],names=c('1950-1977','1978-1988','1989-2013'),xlab="Year",ylab="zooplankton biomass in California")
```

Figure 14. Box and whisker plots of common murre (a), marbled murrelet (b), double-crested cormorant (c) and all three species of birds combined (d) over three time periods

```
par(mfrow=c(2,2))
```

```
boxplot(murre$all[1:29],murre$all[30:40],murre$all[41:66],names=c('1949-1977','1978-1988','1989-2014'),xlab="Year",ylab="common murre (per party hour)")
```

```
boxplot(murrelet$all[20:58],murrelet$all[59:69],murrelet$all[70:95],names=c('1939-1977','1978-1988','1989-2014'),xlab="Year",ylab="marbled murrelet (per party hour)")
```

```
boxplot(cormorant$all[7:43],cormorant$all[44:54],cormorant$all[55:80],names=c('1941-1977','1978-1988','1989-2014'),xlab="Year",ylab="double-crested cormorant (per party hour)")
```

```
boxplot(totalbird[1:28],totalbird[29:39],totalbird[40:63],names=c('1950-1977','1978-1988','1989-2012'),xlab="Year",ylab="All bird species (per party hour)")
```

Bibliography

- Ainley D, Spear L, Allen S and Ribic C (1996) Temporal and spatial patterns in the diet of the common murre in California waters. *Condor* 98(4): 691–705: doi:10.2307/1369852.
- Ainley DG and Hyrenbach DK (2010) Top-down and bottom-up factors affecting seabird population trends in the California current system (1985-2006). *Progress in Oceanography*. Elsevier Ltd 84(3-4): 242–254: doi:10.1016/j.pocean.2009.10.001.
- Barron JA and Anderson L (2010) Enhanced Late Holocene ENSO/PDO expression along the margins of the eastern North Pacific. *Quaternary International* 235: 3–12: doi:10.1016/j.quaint.2010.02.026.
- Becker BH and Beissinger SR (2006) Centennial decline in the trophic level of an endangered seabird after fisheries decline. *Conservation Biology* 20(2): 470–479: doi:10.1111/j.1523-1739.2006.00379.x.
- Benson AJ and Trites AW (2002) Ecological effects of regime shifts in the Bering Sea and eastern North Pacific Ocean. *Fish and Fisheries* 3: 95–113: doi:10.1046/j.1467-2979.2002.00078.x.
- Biggs R, Carpenter SR and Brock WA (2009) Turning back from the brink: detecting an impending regime shift in time to avert it. *Proceedings of the National Academy of Sciences of the United States of America* 106(3): 826–831: doi:10.1073/pnas.0811729106.
- Bond NA, Overland JE, Spillane M and Stabeno P (2003) Recent shifts in the state of the North Pacific. *Geophysical Research Letters* 30(23): 2–5: doi:10.1029/2003GL018597.
- Bracis C (2010) A model of the ocean migration of Pacific salmon. Master of Science thesis, University of Washington.
- Brock WA and Carpenter SR (2010) Interacting regime shifts in ecosystems: implication for early warnings. *Ecological Monographs* 80(3): 353–367.
- Brown E, Colling A, Park D, Phillips J, Rothery D and Wright J (2001) *Ocean Circulation*. Oxford, UK: Butterworth-Heinemann and The Open University.
- Cairns DK (1992) Bridging the gap between ornithology and fisheries science: use of seabird data in stock assessment models. *Condor* 94(4): 811–824: doi:10.2307/1369279.
- CalCOFI (2015) *Zooplankton Data*. Accessed on 02/10/2014. Available at: <http://www.calcofi.org/new.data/index.php/zooplankton/zooplankton-data>.
- Carter H and Kuletz K (1995) Chapter 26: Mortality of Marbled Murrelets due to oil pollution in North America. *USDA Forest Service Gen. Tech. Rep.* 261–270.

Carter HR and Erickson RA (1992) Status and conservation of the marbled murrelet in California 1892-1987. *Proceedings of the Western Foundation of Vertebrate Zoology* 5: 92–116.

Carter HR, McAllister MLC and Isleib ME (1995a) Chapter 27 Mortality of Marbled Murrelets in Gill Nets in North America. *USDA Forest Service Technical Report*, 271–283.

Carter HR, Sowls AL, Rodway MS, Wilson UW, Lowe RW, Mcchesney GJ, et al. (1995b) Population Size, Trends, and Conservation Problems of the Double-Crested Cormorant on the Pacific Coast of North America. *Colonial Waterbirds* 18: 189–215.

Chapdelaine G and Rail J-F (1997) Relationship between cod fishery activities and the population of herring gulls on the North Shore of the Gulf of St Lawrence, Québec, Canada. *ICES Journal of Marine Science* 54 : 708–713: doi:10.1006/jmsc.1997.0248.

Chavez F, Ryan J, Lluch-Cota SE and Ñiquen MC (2003) From Anchovies to Sardines and Back : Multidecadal Change in the Pacific Ocean. *Science* 299(5604): 217–221.

Checkley DM and Barth JA (2009) Patterns and processes in the California Current System. *Progress in Oceanography*. Elsevier Ltd 83(1-4): 49–64: doi:10.1016/j.pocean.2009.07.028.

Chiba S, Batten SD, Yoshiki T, Sasaki Y, Sasaoka K, Sugisaki H, et al. (2015) Temperature and zooplankton size structure : climate control and basin-scale comparison in the North Pacific. *Ecology and Evolution* 1–11: doi:10.1002/ece3.1408.

Collins M, An S-I, Cai W, Ganachaud A, Guilyardi E, Jin F-F, et al. (2010) The impact of global warming on the tropical Pacific Ocean and El Niño. *Nature geoscience* 3: 391–397: doi:10.1038/ngeo868.

Contamin R and Ellison AM (2009) Indicators of Regime Shifts in Ecological Systems : What Do We Need to Know and When Do We Need to Know It ? *Ecological Applications* 19(3): 799–816.

De Graaf RM, Tilghman NG and Anderson SH (1985) Foraging guilds of North American birds. *Environmental Management* 9(6): 493–536: doi:10.1007/BF01867324.

Deng W, Wei G, Xie L, Ke T, Wang Z, Zeng T, et al. (2013) Variations in the Pacific Decadal Oscillation since 1853 in a coral record from the northern South China Sea. *Journal of Geophysical Research: Oceans* 118: 2358–2366: doi:10.1002/jgrc.20180.

Deriso RB, Maunder MN and Pearson WH (2008) Incorporating covariates into fisheries stock assessment models with application to pacific herring. *Ecological Applications* 18(5): 1270–1286: doi:10.1890/07-0708.1.

Di Lorenzo E and Ohman MD (2013) A double-integration hypothesis to explain ocean ecosystem response to climate forcing. *Proceedings of the National Academy of Sciences of the United States of America* 110: 2496–9: doi:10.1073/pnas.1218022110.

Dittman A and Quinn T (1996) Homing in Pacific salmon: mechanisms and ecological basis. *The Journal of experimental biology* 199: 83–91.

Doney SC and Sailley SF (2013) When an ecological regime shift is really just stochastic noise. *Proceedings of the National Academy of Sciences of the United States of America* 110(7): 2438–9: doi:10.1073/pnas.1222736110.

Douville H, Voltaire A and Geoffroy O (2015) The recent global warming hiatus: What is the role of Pacific variability? *Geophysical Research Letters* 42(3): 880–888: doi:10.1002/2014GL062775.

Drake DC and Naiman RJ (2007) Reconstruction of Pacific salmon abundance from riparian tree-ring growth. *Ecological Applications* 17(5): 1523–1542.

Drake DC, Naiman RJ and Helfield JM (2002) Reconstructing salmon abundance in rivers: An initial dendrochronological evaluation. *Ecology* 83(11): 2971–2977.

Drinkwater KF, Beaugrand G, Kaeriyama M, Kim S, Ottersen G, Perry RI, et al. (2010) On the processes linking climate to ecosystem changes. *Journal of Marine Systems*. Elsevier B.V. 79(3-4): 374–388: doi:10.1016/j.jmarsys.2008.12.014.

Du X, Peterson W and O'Higgins L (2015) Interannual variations in phytoplankton community structure in the northern California Current during the upwelling seasons of 2001-2010. *Marine Ecology Progress Series* 519: 75–87: doi:10.3354/meps11097.

Duffy PA, Walsh JE, Graham JM, Mann DH and Rupp TS (2005) Impacts of large-scale atmospheric-ocean variability on Alaskan fire season severity. *Ecological Applications* 15(4): 1317–1330: doi:10.1890/04-0739.

Eggers DM, Irvine JR, Fukuwaka M and Karpenko VI (2005) Catch Trends and Status of North Pacific Salmon. *NPAFC Document* 723(3): 1–35.

Emmett RL, Brodeur RD, Miller TW, Pool SS, Krutzikowsky GK, Bentley PJ, et al. (2005) Pacific Sardine (*Sardinops Sagax*) Abundance, Distribution, and Ecological Relationships in the Pacific Northwest. *CalCOFI Report* 46: 122–143.

Francis RC, Hare SR, Hollowed AB and Wooster WS (1998) Effects of interdecadal climate variability on the oceanic ecosystems of the NE Pacific. *Fisheries Oceanography* 7(1): 1–21.

García-Reyes M, Largier JL and Sydeman WJ (2014) Synoptic-scale upwelling indices and predictions of phyto- and zooplankton populations. *Progress in Oceanography* 120: 177–188: doi:10.1016/j.pocean.2013.08.004.

Geiger HJ, Perry T, Fukuwaka M and Radchenko V (2002) Status of Salmon Stocks and Fisheries in the North Pacific Ocean. *NPAFC Technical Report* (4): 6–7.

Goodrich GB (2004) Modulation of the Winter ENSO Arizona Climate Signal by the Pacific Decadal Oscillation. *Journal of the Arizona-Nevada Academy of Science* 36(2): 88–94.

Google Maps (2015) *West Coast of North America*. Accessed on 25/08/2015. Available at: <https://www.google.co.uk/maps/@52.8382004,-2.3278149,6z?hl=en>

Guénette S, Araújo JN and Bundy A (2014) Exploring the potential effects of climate change on the Western Scotian Shelf ecosystem, Canada. *Journal of Marine Systems*. Elsevier B.V. 134: 89–100: doi:10.1016/j.jmarsys.2014.03.001.

Hare SR and Mantua NJ (2000) Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Progress in Oceanography* 47: 103–145: doi:10.1016/S0079-6611(00)00033-1.

Hare SR, Mantua NJ and Francis RC (1999) Inverse production regimes : Alaska and West Coast Pacific Salmon. *Fisheries* 1–34.

Harrison DE and Chiodi AM (2014) Multi-decadal variability and trends in the El Nino-Southern Oscillation and tropical Pacific fisheries implications. *Deep-Sea Research Part II: Topical Studies in Oceanography*. Elsevier 1–13: doi:10.1016/j.dsr2.2013.12.020.

Hasselmann K (1982) An ocean model for climate variability studies. *Progress in Oceanography* 11(1976): 69–92.

Helsel DR and Hirsch RM (1992) Chapter 12: Trend Analysis. *Statistical Methods in Water Resources*. Elsevier, 323–355.

Henderson EE, Forney KA, Barlow JP, Hildebrand JA, Douglas AB, Calambokidis J, et al. (2014) Effects of fluctuations in sea-surface temperature on the occurrence of small cetaceans off Southern California. *Fishery Bulletin* 112: 159–177: doi:10.7755/FB.112.2-3.5.

Hessl AE, McKenzie D and Schellhaas R (2004) Drought and Pacific Decadal Oscillation Linked to Fire Occurrence in the Inland Pacific Northwest. *Ecological Applications* 14(2): 425–442.

Heymans JJ, Guénette S and Christensen V (2007) Evaluating network analysis indicators of ecosystem status in the Gulf of Alaska. *Ecosystems* 10(3): 488–502: doi:10.1007/s10021-007-9034-y.

Hipfner JM (2005) Population status of the Common Murre *Uria aalge* in British Columbia, Canada. *Marine Ornithology* 33: 67–70.

Hirata T, Hardman-Mountford NJ, Barlow R, Lamont T, Brewin R, Smyth T, et al. (2009) An inherent optical property approach to the estimation of size-

specific photosynthetic rates in eastern boundary upwelling zones from satellite ocean colour: An initial assessment. *Progress in Oceanography*. Elsevier Ltd 83: 393–397: doi:10.1016/j.pocean.2009.07.019.

Hsieh C, Glaser SM, Lucas AJ and Sugihara G (2005) Distinguishing random environmental fluctuations from ecological catastrophes for the North Pacific Ocean. *Nature* 435(May): 336–340: doi:10.1038/nature03553.

Hsieh CH and Ohman MD (2006) Biological responses to environmental forcing: The linear tracking window hypothesis. *Ecology* 87(8): 1932–1938: doi:10.1890/0012-9658(2006)87[1932:BRTEFT]2.0.CO;2.

IPCC (2013) *Summary for Policymakers. In: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, UK: Cambridge University Press: doi:10.1017/CBO9781107415324.

Irvine JR and Fukuwaka MA (2011) Pacific salmon abundance trends and climate change. *ICES Journal of Marine Science* 68(6): 1122–1130.

Johnstone JA and Mantua NJ (2014) Atmospheric controls on northeast Pacific temperature variability and change, 1900–2012. *Proceedings of the National Academy of Sciences* 111(40): 14360–14365: doi:10.1073/pnas.1318371111.

Kalkstein AJ and Goodrich GB (2012) The Effect of ENSO and PDO on Three Airborne Pollutants in Phoenix, Arizona. *Journal of the Arizona-Nevada Academy of Science* 43(2): 91–98: doi:10.2181/036.043.0205.

King CAM (1965) *Oceanography for Geographers*. Chatham, UK: W. and J. Mackay and Co Ltd.

Kufs C (2011) *Stats with Cats: The Domesticated Guide to Statistics, Models, Graphs and other Breeds of Data Analysis*. Tucson, Arizona: Wheatmark.

Lenton TM, Held H, Kriegler E, Hall JW, Lucht W, Rahmstorf S, et al. (2008) Tipping elements in the Earth's climate system. *Proceedings of the National Academy of Sciences of the United States of America* 105(6): 1786–1793: doi:10.1073/pnas.0705414105.

Levin PS (2003) Regional differences in responses of chinook salmon populations to large-scale climatic patterns. *Journal of Biogeography* 30(5): 711–717.

Litzow MA and Mueter FJ (2014) Assessing the ecological importance of climate regime shifts: An approach from the North Pacific Ocean. *Progress in Oceanography*. Elsevier Ltd 120: 110–119: doi:10.1016/j.pocean.2013.08.003.

Litzow MA, Mueter FJ and Hobday AJ (2014) Reassessing regime shifts in the North Pacific: Incremental climate change and commercial fishing are necessary for explaining decadal-scale biological variability. *Global Change Biology* 20: 38–50: doi:10.1111/gcb.12373.

- Maher N, Gupta AS and England MH (2014) Drivers of decadal hiatus periods in the 20th and 21st centuries. *Geophysical Research Letters* 41: 5978–5986: doi:10.1002/2014GL060527.
- Mantua NJ (2002) Pacific Decadal Oscillation (PDO). In: MacCracken MC and Perry JS (eds) *Encyclopedia of Global Environmental Change*. Chichester: John Wiley and Sons Ltd, 592–594.
- Mantua NJ (2015) *PDO Index*. Accessed on 04/02/2015. Available at: <http://jisao.washington.edu/pdo/PDO.latest>.
- Mantua NJ and Hare SR (2002) The Pacific Decadal Oscillation. *Journal of Oceanography* 58(1): 35–44.
- Mantua NJ, Hare SR, Zhang Y, Wallace JM and Francis RC (1997) A Pacific Interdecadal Climate Oscillation with Impacts on Salmon Production. *Bulletin of the American Meteorological Society* 78(6): 1069–1079: doi:10.1175/1520-0477(1997)078<1069:APICOW>2.0.CO;2.
- Marshall DB (1988) Status of the Marbled Murrelet in North America: with special emphasis on populations in California, Oregon, and Washington. *U.S. Fish Wildl. Serv. Biol. Rep.* 88(August): 1–19.
- Masuda S (2002) Role of the ocean in the decadal climate change in the North Pacific. *Journal of Geophysical Research* 107: 1–18: doi:10.1029/2002JC001420.
- Matthews DR (1983) Feeding ecology of the common murre *Uria aalga* off the Oregon coast. Master of Science dissertation, Department of Biology, University of Oregon.
- McGowan JA, Bograd SJ, Lynn RJ and Miller AJ (2003) The biological response to the 1977 regime shift in the California Current. *Deep-Sea Research Part II: Topical Studies in Oceanography* 50: 2567–2582: doi:10.1016/S0967-0645(03)00135-8.
- McLeod AI (2011) Kendall: Kendall rank correlation and Mann-Kendall trend test. R package version 2.2.
- Menge BA, Chan F, Nielsen KJ, Lorenzo E Di and Lubchenco J (2009) Climatic variation alters supply-side ecology: Impact of climate patterns on phytoplankton and mussel recruitment. *Ecological Monographs* 79(3): 379–395.
- Met Office (2015) *Hadley Centre Sea Ice and Sea Surface Temperature data set (HadISST)*. . Available at: <http://www.metoffice.gov.uk/hadobs/hadisst/>.
- Mollmann C, Folke C, Edwards M and Conversi A (2015) Marine regime shifts around the globe : theory, drivers and impacts. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* 370.
- Monaghan P (1996) Relevance of the behaviour of seabirds to the conservation of marine environments. *77*: 227–237: doi:10.2307/3546061.

- Monastersky R (2000) Major mood swing alters Pacific character. *Science News* 157(5): 69.
- NASA (2015) Ocean Motion and Surface Currents: Upwelling and Downwelling background. Accessed on 22/08/2015. Available at: <http://oceanmotion.org/html/background/upwelling-and-downwelling.htm>
- National Audubon Society (2015) *The Christmas Bird Count Historical Results*. Accessed on 20/10/2014. Available at: <http://www.christmasbirdcount.org>.
- Neira S, Moloney CL, Cury P, Mullon C and Christensen V (2009) Mechanisms affecting recovery in an upwelling food web: The case of the southern Humboldt. *Progress in Oceanography*. Elsevier Ltd 83(1-4): 404–416: doi:10.1016/j.pocean.2009.07.007.
- Nelson SK and Hamer TE (1995) Nest Success and the Effects of Predation on Marbled Murrelets. *USDA Forest Service Technical Report*, 89–98.
- NOAA (2015a) *Commercial Fisheries Statistics: Annual Commercial Landing Statistics*. Accessed on 06/10/2014. Available at: <http://www.st.nmfs.noaa.gov/commercial-fisheries/commercial-landings/annual-landings/index>.
- NOAA (2015b) *Commercial Fisheries Statistics: Data Caveats*. Accessed on 03/11/2014. Available at: <http://www.st.nmfs.noaa.gov/commercial-fisheries/commercial-landings/data-caveats/index>.
- O'Hara RB and Kotze DJ (2010) Do not log-transform count data. *Methods in Ecology and Evolution* 1: 118–122: doi:10.1111/j.2041-210X.2010.00021.x.
- Ohman MD and Smith PE (1995) A comparison of zooplankton sampling methods in the CalCoFI time series. *California Cooperative Oceanic Fisheries Investigations Report* 36: 153–158.
- Overland JE, Alheit J, Bakun A, Hurrell JW, Mackas DL and Miller AJ (2010) Climate controls on marine ecosystems and fish populations. *Journal of Marine Systems*. Elsevier B.V. 79(3-4): 305–315: doi:10.1016/j.jmarsys.2008.12.009.
- Overland JE, Percival DB and Mofjeld HO (2006) Regime shifts and red noise in the North Pacific. *Deep-Sea Research Part I: Oceanographic Research Papers* 53(4): 582–588: doi:10.1016/j.dsr.2005.12.011.
- Overland JE and Wang M (2007) Future Climate of the North Pacific Ocean. *Eos* 88(16).
- Paine RT, Wootton JT and Boersma PD (1990) Direct and indirect effects of peregrine falcon predation on seabird abundance. *The Auk* 107(1): 1–9.
- Parrish JK, Marvier M and Paine RT (2001) Direct and Indirect Effects: Interactions between Bald Eagles and Common Murres. *Ecological Applications* 11: 1858–1869.

Parrish JK and Zador SG (2003) Seabirds as indicators: An exploratory analysis of physical forcing in the Pacific Northwest coastal environment. *Estuaries* 26(4): 1044–1057: doi:10.1007/BF02803362.

Peery MZ, Beissinger SR, Burkett E, Newman SH, Zachariah M and Beissinger R (2006) Local survival of marbled murrelets in central California: Roles of oceanographic processes, sex and radiotagging. *The Journal of Wildlife Management* 70(1): 78–88.

Petersen JK, Hansen JW, Laursen MB, Clausen P, Carstensen J and Conley DJ (2008) Regime shift in a coastal marine ecosystem. *Ecological applications : a publication of the Ecological Society of America* 18(2): 497–510: doi:10.1890/07-0752.1.

Piatt JF and Anderson P (1996) Response of Common Murres to the Exxon Valdez Oil Spill and Long-Term Changes in the Gulf of Alaska Marine Ecosystem. *American Fisheries Society Symposium*, 720–737.

Piatt JF and Naslund NL (1995) Chapter 28 Abundance, Distribution, and Population Status of Marbled Murrelets in Alaska. *USDA Forest Service Technical Report*.

Putman NF, Scanlan MM, Billman EJ, O’Neil JP, Couture RB, Quinn TP, et al. (2014) An inherited magnetic map guides ocean navigation in juvenile pacific salmon. *Current Biology*. Elsevier Ltd 24(4): 446–450: doi:10.1016/j.cub.2014.01.017.

R Core Team (2014) R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Raphael MG, Mack DE and Cooper BA (2002) Landscape-scale Relationships between Abundance of Marbled Murrelets and Distribution of Nesting Habitat. *The Condor* 104(2): 331–342.

Rayner NA, Parker DE, Horton EB, Folland CK, Alexander LV and Rowell DP (2003) Global analyses of sea surface temperature, sea ice, and night marine air temperature since the late nineteenth century. *Journal of Geophysical Research* 108.

Rodway MS, Carter HR, Sealy SG and W. CR (1992) Status of the marbled murrelet in British Columbia. *Proceedings of the Western Foundation of Vertebrate Zoology* 5(1): 17–41.

Roemmich D and McGowan J (1995) Climatic warming and the decline of zooplankton in the california current. *Science* 267(5202): 1324–1326.

Rudnick DL and Davis RE (2003) Red noise and regime shifts. *Deep-Sea Research Part I: Oceanographic Research Papers* 50(6): 691–699: doi:10.1016/S0967-0637(03)00053-0.

Salinger MJ (2013) A brief introduction to the issue of climate and marine fisheries. *Climatic Change* 119: 23–35: doi:10.1007/s10584-013-0762-z.

Scheffer M, Bascompte J, Brock W a, Brovkin V, Carpenter SR, Dakos V, et al. (2009) Early-warning signals for critical transitions. *Nature* 461(7260): 53–59: doi:10.1038/nature08227.

Scheffer M, Carpenter S, Foley J a, Folke C and Walker B (2001) Catastrophic shifts in ecosystems. *Nature* 413(October): 591–596: doi:10.1038/35098000.

Scheffer M and Carpenter SR (2003) Catastrophic regime shifts in ecosystems: Linking theory to observation. *Trends in Ecology and Evolution* 18(12): 648–656: doi:10.1016/j.tree.2003.09.002.

Scott JM, Wiens J a and Claeys RR (1975) Organochlorine Levels Associated with a Common Murre Die-off in Oregon. *The Journal of Wildlife Management* 39(2): 310–320: doi:10.2307/3799908.

Sissenwine M and Symes D (2007) Reflections on the Common Fisheries Policy. *The General Directorate for Fisheries and Maritime Affairs of the European Commission*.

Soares HC, Gherardi DFM, Pezzi LP, Kayano MT and Paes ET (2014) Patterns of interannual climate variability in large marine ecosystems. *Journal of Marine Systems*. Elsevier B.V. 134: 57–68: doi:10.1016/j.jmarsys.2014.03.004.

Speckman SG, Speckman SG, Springer AM, Springer AM, Piatt JF, Piatt JF, et al. (2000) Temporal Variability in Abundance of Marbled Murrelets at Sea in Southeast Alaska. *Waterbirds* 23(3): 364–377.

Steele JH (1977) Chapter 13: Ecological modelling of the upper layers. In: Kraus EB (ed) *Modelling and prediction of the upper layers of the ocean*. Exeter: Pergamon Press.

Steele JH (1998) Regime shifts in marine ecosystems. *Ecological Applications* 8(1): S33–S36.

Steele JH, Henderson EW, Mangel M and Clark C (1994) Coupling between Physical and Biological Scales. *Philosophical Transactions of the Royal Society B: Biological Sciences* 343(1303): 5–9: doi:10.1098/rstb.1994.0001.

Sydeman WJ, Hester MM, Thayer JA, Gress F, Martin P and Buffa J (2001) Climate change, reproductive performance and diet composition of marine birds in the southern California Current system, 1969-1997. *Progress in Oceanography* 49: 309–329: doi:http://dx.doi.org/10.1016/S0079-6611(01)00028-3.

Sydeman WJ, Hobson KA, Pyle P and McLaren EB (1997) Trophic relationships among seabirds in central California: Combined stable isotope and conventional dietary approach. *Condor* 99(2): 327–336: doi:10.2307/1369938.

Sydeman WJ, Santora JA, Thompson SA, Marinovic B and Lorenzo E Di (2013) Increasing variance in North Pacific climate relates to unprecedented ecosystem variability off California. *Global Change Biology* 19(6): 1662–1675: doi:10.1111/gcb.12165.

- Thomas AC, Brickley P and Weatherbee R (2009) Interannual variability in chlorophyll concentrations in the Humboldt and California Current Systems. *Progress in Oceanography*. Elsevier Ltd 83: 386–392: doi:10.1016/j.pocean.2009.07.020.
- Thompson DM, Cole JE, Shen GT, Tudhope AW and Meehl G a (2015) Early twentieth-century warming linked to tropical Pacific wind strength. *Nature geoscience* 8: 117–121: doi:10.1038/NGEO2321.
- Tomczak M and Godfrey JS (1994) *Regional Oceanography: An Introduction*. Oxford, UK: Pergamon.
- Townsend DW (2012) *Oceanography and Marine Biology: An introduction to marine science*. Sinauer Associates.
- U.S. Fish and Wildlife Service (2005) Regional Seabird Conservation Plan, Pacific Region.
- United Nations (2013) *The United Nations Convention on the Law of the Sea, Part V, Exclusive Economic Zone. Oceans and Law of the Sea*. Accessed on 30/10/2014. Available at: http://www.un.org/Depts/los/convention_agreements/texts/unclos/part5.htm.
- Vance TR, Roberts JL, Plummer CT, Kiem AS and van Ommen TD (2015) Interdecadal Pacific variability and eastern Australian megadroughts over the last millennium. *Geophysical Research Letters* 42(1): 129–137: doi:10.1002/2014GL062447.
- Vandenbosch R (2000) Effects of ENSO and PDO events on seabird populations as revealed by Christmas bird count data. *Waterbirds* 23(3): 416–422: doi:10.2307/1522178.
- Varotsos CA, Efstathiou MN and Cracknell AP (2015) Sharp rise in hurricane and cyclone count during the last century. *Theoretical and Applied Climatology* 119: 629–638: doi:10.1007/s00704-014-1136-9.
- Varoujean II DH and Williams WA (1995) Abundance and distribution of Marbled Murrelets in Oregon and Washington based on aerial surveys. *Ecology and conservation of the Marbled Murrelet. USDA Forest Service General Technical Report* 327–337.
- Veit RR, Pyle P and McGowan JA (1996) Ocean warming and long-term change in pelagic bird abundance within the California current system. *Marine Ecology Progress Series* 139: 11–18.
- Velarde E, Tordesillas MDLS and Rocio Esquivel LV (1994) Seabirds as indicators of important fish populations in the Gulf of California. *CalCOFI Report* 35: 137–143.
- Watanabe T and Yamazaki K (2014) Decadal-scale variation of South Asian summer monsoon onset and its relationship with the pacific decadal oscillation. *Journal of Climate* 27: 5163–5173: doi:10.1175/JCLI-D-13-00541.1.

Wen C, Kumar A and Xue Y (2014) Factors contributing to uncertainty in Pacific Decadal Oscillation index. *Geophysical Research Letters* 41: 7980–7986: doi:10.1002/2014GL061992.

Woodward FI, Lomas MR and Quaife T (2008) Global responses of terrestrial productivity to contemporary climatic oscillations. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* 363(1504): 2779–2785: doi:10.1098/rstb.2008.0017.

Yamazaki H and Kamykowski D (1991) The vertical trajectories of motile phytoplankton in a wind-mixed water column. *Deep-sea Research* 38(2): 219–241

Yim BY, Kwon M, Min HS and Kug J-S (2015) Pacific Decadal Oscillation and its relation to the extratropical atmospheric variation in CMIP5. *Climate Dynamics* 44(5-6): 1521–1540: doi:10.1007/s00382-014-2349-4.

Zongshang SI and Yongsheng XU (2014) Influence of the Pacific Decadal Oscillation on regional sea level rise in the Pacific Ocean from 1993 to 2012. *Chinese Journal of Oceanology and Limnology* 32(6): 1414–1420.

Zwolinski JP and Demer DA (2014) Environmental and parental control of Pacific sardine (*Sardinops sagax*) recruitment. *ICES Journal of Marine Science* 71(8): 2198–2207: doi:10.1093/icesjms/fst048.