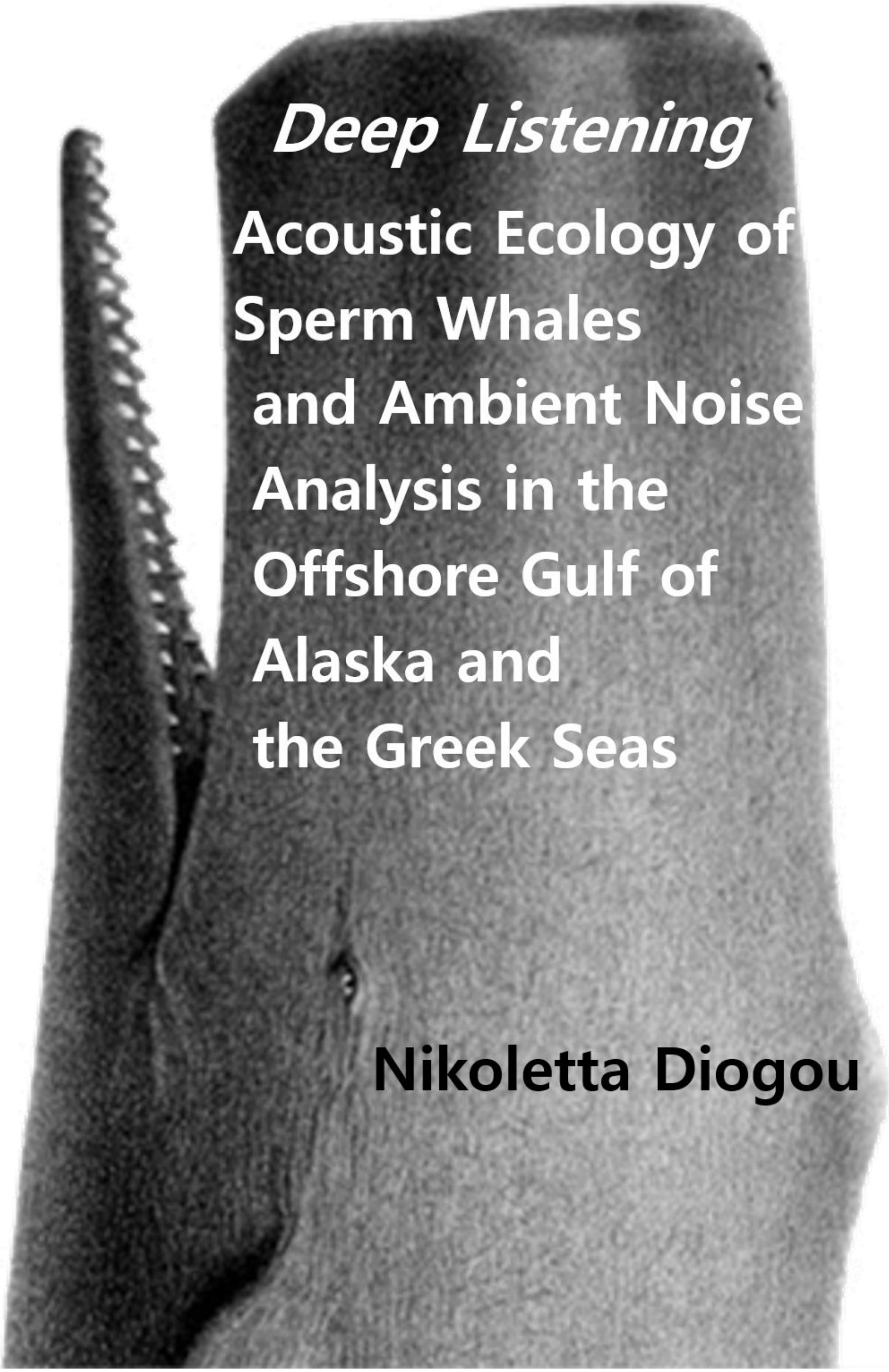

Deep Listening

Acoustic Ecology of Sperm Whales and Ambient Noise Analysis in the Offshore Gulf of Alaska and the Greek Seas

Nikoletta Diogou

ΠΑΝΕΠΙΣΤΗΜΙΟ
ΑΙΓΑΙΟΥ

ΤΜΗΜΑ ΩΚΕΑΝΟΓΡΑΦΙΑΣ ΚΑΙ ΘΑΛΑΣΣΙΩΝ ΒΙΟΕΠΙΣΤΗΜΩΝ

ΔΙΔΑΚΤΟΡΙΚΗ ΔΙΑΤΡΙΒΗ ΜΕ ΘΕΜΑ

Ακουστική Οικολογία του Φυσητήρα (*Physeter macrocephalus*) και Ανάλυση Περιβαλλοντικού Θορύβου στον Κόλπο της Αλάσκας και στις Ελληνικές Θάλασσες

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List of Abbreviations and Symbols used

a	Number of subsamples within each sound bite
AICc	Akaike Information Criterion for small samples
ARMA	Autoregressive Moving Average
b	duration of one of the eight subsamples in each sound bite
BVF	Brunt–Väisälä Frequency
c	Click duration
CCF	Cross-Correlation Function
CHL	Chlorophyll-*a* concentration
Cp	Specific heat of seawater
D	Current direction
D	the sum of the possible instances that a click could overlap with one of the eight subsamples of a sound bite
dz	Depth interval
EKE	Eddy Kinetic Energy
ENSO	El Niño–Southern Oscillation

FULL	‘Full model’ with *in situ* and remotely sensed variables
GLS	Generalized Least Squares
GOA	Gulf of Alaska
h	Depth across which there is minimal heat transfer
HC	Ocean Heat Content
ICI	Inter Click Interval
intBVF75	Integrated Brunt–Väisälä frequency for the 0-75 m pycnocline
IS	‘*In situ* model’ with only *in situ* variables
km	Kilometers
m	Meters
maxBVF	Strength of the permanent pycnocline
ODV	Ocean Data View
ONI	Oceanic Niño Index
OSP	Ocean Station PAPA
P	Probability detecting different numbers of sperm whales
PACF	Partial Autocorrelation Function

PAL	Passive Aquatic Listener
PDO	Pacific Decadal Oscillation
P_n	Probability of detecting sperm whales
Q-Q	Quantile-Quantile
RMS	Root-Mean-Square
RS	‘Remote Sense model’ with only remotely sensed variables
S	Current Speed
SPD	Spectral Probability Density plots
SST	Sea Surface Temperature
SSTsd	Standard Deviation of Sea Surface Temperature
T	Duration of each ICI examined
T(z)	Temperature at each depth interval
U	Zonal current component
u	Zonal geostrophic currents
V	Meridional current component
v	Meridional geostrophic currents

VIF	Variance Inflation Factor
WUP	Ekman Upwelling
Zmax	Depth of maximum Brunt–Väisälä frequency for the 81-200 m
ΔAICc	AICc difference to the minimum AICc score
ρ	Mean density of seawater

Γλωσσάρι Ακουστικής Ορολογίας

Acoustic Sensor	Ακουστικός αισθητήρας
Ambient Noise Levels	Περιβαλλοντικά Επίπεδα Θορύβου
Animal-borne tags	Ραδιοπομποί τοποθετημένοι στο σώμα των ζώων
Automatic Detection Algorithm	Αυτόματος αλγόριθμος ανίχνευσης
Bioacoustics	Βιοακουστική
Buoy Mounted Autonomous Recorder	Αυτόνομος καταγραφέας τοποθετημένος σε σημαδούρα
Cabled seafloor arrays	Σειρά Δικτυωμένων Υδροφώνων
Click trains	Αλληλουχία από κλικς
Detectability	Ανιχνευσιμότητα
Detection Range	Απόσταση Ανίχνευσης Ακουστικού Σήματος
Detection threshold	Όριο έντασης μέχρι το οποίο ανιχνεύεται ένα ακουστικό σήμα
Directional	Κατευθυντικό

Echolocation	Ηχοεντοπισμός
Energy detector	Ενεργειακός Ανιχνευτής
Frequency band	Εύρος Συχνότητας
Hydrophone	Υδρόφωνο
Inter-Click-Interval	Χρονική απόσταση ανάμεσα στα κλικς
Localization	Εντοπισμός ακουστικής πηγής
Omnidirectional	Πανκατευθυντικό
Passive Acoustic Monitoring	Παθητική Ακουστική Παρακολούθηση
Passive Aquatic Listener	Παθητικός Υδροκαταγραφέας
Peak Frequency	Συχνότητα που συγκεντρώνεται η περισσότερη ενέργεια
Sampling Rate	Συχνότητα δειγματοληψίας
Signal-to-noise-ratio	Αναλογία μεταξύ ακουστικού σήματος και θορύβου
Sound bite	Ακουστικό Δείγμα
Sound Propagation Conditions	Συνθήκες Διάδωσης του Ήχου
Soundscape	Ηχοτοπίο

Source level	Ένταση του Ήχου στο ένα μέτρο από την πηγή του ήχου
Spectral probability density plots	Γραφήματα με την Κατανομή της Πυκνότητας Πιθανότητας Έντασης του Ήχου
Spectrogram	Φασματογράφημα
Spectrum	Ενεργειακό Φάσμα
Stationary Signal	Συνεχής ήχος
Towed Hydrophone Arrays	Ρυμουλκώμενα υδροφώνα στη σειρά
Transient Signal	Ασυνεχής/Διακοπτόμενος ήχος
Triggering frequency band	Εύρος συχνότητας που ενεργοποιείται ο ανιχνευτής
Vocalization	Φώνηση
Waveform	Κυματομορφή

Abstract of the dissertation

Sperm whale (*Physeter macrocephalus*) is the largest of odontocetes, and a cosmopolitan species widely distributed in the world oceans. With their populations in the Mediterranean Sea and the United States listed as Endangered, knowledge of the critical habitats, the temporal variability of the habitat use and environmental conditions that define those habitats is fundamental for the conservation efforts of this apex predator.

Known for their extreme diving abilities, sperm whales are difficult to observe visually but their loud and characteristic calls are easily distinguishable acoustically. In this dissertation, an autonomous sub-sampling acoustic recorder was used to investigate the long-term sperm whale presence in three locations in the North Pacific and the Eastern Mediterranean Sea and enrich our understanding of their ecology. By analyzing a year-and-half-long acoustic data set from the Greek seas and a five-year-long acoustic data set from the Gulf of Alaska (GOA), it is demonstrated that sperm whales are present year round at Pylos (Pylos Station of the Hellenic Centre for Marine Research – HCMR) on the Hellenic Trench, and at Ocean Station PAPA (OSP) offshore the GOA. The absence of sperm whale detections in the North Aegean Sea at Athos (Athos Station of the HCMR) was linked to the almost continuous detections of another teuthophageous deep diving odontocete, the Risso's dolphins (*Grampus griseus*), and is likely explained by the differentiation in ecological niche between the two species. Even though sperm whales were detected year-round at Pylos, the number of days with detections was low compared to OSP and that was attributed partly to a smaller population sustained in highly oligotrophic conditions. Additionally, the acoustic dominance of delphinids, which occupied the majority of the acoustic

recordings at Pylos, would cause an underestimation of the sperm whale acoustic presence.

The examinations of temporal patterns showed higher number of detections during late spring and summer at Pylos. The, almost constant, sperm whale presence at OSP presented strong seasonality with significantly higher detection rates during the summer months and lower in the winter. This pattern was linked to the seasonal latitudinal fluctuations of the North Pacific Transition Zone, a source of nutrients and organisms at the North Pacific, and to shifts in the intensity of the Alaska Current. Quantification of the interannual variability of sperm whales at OSP, based on habitat-modeling results, indicated a positive relationship between sperm whale acoustic detections and ocean heating, circulation, and stratification. Further investigations hinted that these oceanographic conditions are characteristics of the relaxation of the Alaska Gyre and the intrusion of coastal mesoscale eddies at OSP, which in turn are associated with stronger El Niño events and warm phases of the PDO. During Los Niños, the Subarctic Frontal Zone and North Pacific Transition Zone migrate northwards transferring prey close to OSP. Therefore, intensification of El Niño events due to climate change is likely to increase sperm whale occurrence at higher latitudes, including the GOA, while food availability reduces in the Tropics. This study is the first to isolate and interpret ecologically the interannual variability of sperm whale acoustic presence in the GOA.

The propagation range of sperm whale usual clicks was calculated, using the BELLHOP models, to vary between 7 and 8 km on average in winter and summer respectively at OSP, and seasonal changes of sound propagation conditions did not influence the detectability of sperm whale calls. At Pylos and Athos, detection distances ranged between 13 and 22 km, and were likely driven by seasonal differences in ambient sound levels. Wind speed was related to the variability in ambient sound levels at both sites at 3 kHz, while shipping noise was more dominant at Pylos in the summer.

Through assessment of the detection performance of the Passive Aquatic Listener (PAL) used, this dissertation identifies PAL to be highly efficient in detecting acoustically dominant cetacean species and suggests specific adjustments on the detection algorithm in order to increase the probability of detecting signals of interest in different soundscapes. Low variability in numbers of whales detected throughout the year, seemed to increase the probability detecting sperm whales above 50% at OSP. However, at Pylos, reduced recording effort during the first nine months had a negative effect on the probability of detecting sperm whale clicks and likely caused an underestimation of the sperm whale acoustic presence in the area. Additionally, this dissertation provides substantial baseline information on the ambient sound levels in all three sites, and raises concerns about the increased noise levels at Pylos, associated with intense shipping traffic. Therefore, sperm whales and all cetacean fauna at the Hellenic Trench are exposed to increased risk of ship strike and noise disturbances.

Together, this study reveals the temporal patterns of sperm whale occurrence in the offshore GOA and the Eastern Mediterranean Sea and attempts to explain the processes behind them. Finally, it highlights the usefulness of long-term acoustic recordings in enhancing the knowledge of sperm whale ecology. Ultimate goal of this work was to contribute to the conservation efforts of the species in both regions.

Σύνοψη

Ο φυσητήρας (*Physeter macrocephalus*) είναι το μεγαλύτερο οδοντοκήτος παγκοσμίως και είδος ευρέως κατανεμημένο σε όλους τους ωκεανούς. Ο πληθυσμός του στη Μεσόγειο και στις Ηνωμένες Πολιτείες Αμερικής θεωρείται ότι βρίσκεται σε κρίσιμα επίπεδα και χαρακτηρίζεται ως είδος υπό εξαφάνιση. Η γνώση σχετικά με τα κρίσιμα ενδιαιτήματά του, την εποχική διακύμανση χρήσης αυτών των ενδιαιτημάτων και τις περιβαλλοντικές συνθήκες που τα χαρακτηρίζουν, είναι πολύ σημαντική για τις προσπάθειες προστασίας και διατήρησης του είδους.

Γνωστοί για την ικανότητα τους να καταδύονται σε μεγάλα βάθη, οι φυσητήρες είναι δύσκολο να εντοπιστούν με τις παραδοσιακές μεθόδους παρακολούθησης, αλλά με δεδομένο ότι παράγουν δυνατές και χαρακτηριστικές φωνήσεις είναι ευκολότερα διακριτοί με ακουστικά μέσα. Σε αυτή τη διατριβή, χρησιμοποιήθηκε ένας αυτόνομος μη-συνεχής ακουστικός καταγραφέας για τη διερεύνηση της μακροχρόνιας παρουσίας φυσητήρων σε τρεις τοποθεσίες στον Βόρειο Ειρηνικό Ωκεανό και στην Ανατολική Μεσόγειο Θάλασσα ώστε να εμπλουτίσουμε τη γνώση σχετικά με την οικολογία τους. Η ανάλυση ακουστικών δεδομένων ενάμιση έτους από τις Ελληνικές θάλασσες και πέντε ετών από τον Κόλπο της Αλάσκας, απέδειξε τη παρουσία των φυσητήρων καθ' όλη τη διάρκεια του έτους στους σταθμούς *Πύλος* (του Ελληνικού Κέντρου Θαλασσίων Ερευνών- ΕΛΚΕΘΕ) στην Ελληνική Τάφρο, και *PAPA* στα ανοιχτά του Κόλπου της Αλάσκας. Η απουσία καταγραφών του είδους στον σταθμό *Άθω* (του ΕΛΚΕΘΕ) στο Βόρειο Αιγαίο Πέλαγος συσχετίστηκε με τη σχεδόν συνεχή ακουστική καταγραφή σταχτοδέλφινων (*Grampus griseus*), τα οποία επίσης τρέφονται με καλαμάρια, και ενδεχομένως καταλαμβάνουν αυτό τον οικότοπο ο οποίος είναι ρηχότερος σε σχέση με τον

καταλληλότερο οικότοπο για τους φυσητήρες. Εάν και ανιχνεύτηκαν φυσητήρες σε όλους του μήνες του χρόνου στη Πύλο, ο αριθμός των ημερών με ανίχνευση ήταν πολύ μειωμένος (κατά 7 φορές περίπου) σε σχέση με τον σταθμό PAPA, και αυτό αποδίδεται στο σημαντικά μικρότερο πληθυσμό φυσητήρων σε μια έντονα ολιγοτροφική περιοχή, αλλά και στην ακουστική επικράτηση δελφινοειδών που ενδεχομένως προκάλεσαν την υποτίμηση της ακουστικής παρουσίας των φυσητήρων. Στην Πύλο καταγράψαμε και κοινωνικές ομάδες με θηλυκά άτομα, ενώ η PAPA αποτελεί πιθανότατα ενδιαίτημα αποκλειστικά αρσενικών φυσητήρων, καθώς δεν καταγράφηκαν φωνήσεις τύπου codas που σχετίζονται με τις κοινωνικές ομάδες.

Η διερεύνηση εποχικών μοτίβων έδειξε περισσότερες ανιχνεύσεις κατά τη διάρκεια της άνοιξης και του καλοκαιριού στην Πύλο. Η σχεδόν συνεχής παρουσία φυσητήρων στον σταθμό PAPA στον Ειρηνικό Ωκεανό παρουσίασε έντονη εποχικότητα με σημαντικά υψηλότερο αριθμό ανιχνεύσεων κατά τους καλοκαιρινούς μήνες και χαμηλότερο αριθμό κατά τους χειμερινούς μήνες. Αυτό το μοτίβο συνδέθηκε τόσο με τις εποχικές γεωγραφικές διακυμάνσεις της Ζώνης Μετάβασης του Βορείου Ειρηνικού (North Pacific Transition Zone) που αποτελεί πηγή θρεπτικών και οργανισμών στο Βόρειο Ειρηνικό, όσο και στις αλλαγές στην ένταση του Ρεύματος της Αλάσκας (Alaska Current). Η Ζώνη Μετάβασης του Βορείου Ειρηνικού μετακινείται κατά 1000 km περίπου βορειότερα το καλοκαίρι, καλύπτοντας την περιοχή που βρίσκεται ο σταθμός PAPA. Με την ίδια περιοδικότητα μετακινείται και ένα είδος καλαμαριού που αποτελεί σημαντική τροφή για τους φυσητήρες στον Ειρηνικό. Η ποσοτικοποίηση της διακύμανσης της παρουσίας των φυσητήρων στον σταθμό PAPA μεταξύ των διαφορετικών χρόνων, μέσω των αποτελεσμάτων από τη μοντελοποίηση ενδιαιτήματος, υπέδειξε μια θετική σχέση ανάμεσα στη παρουσία των ζώων και τη θέρμανση του ωκεανού, τη κυκλοφορία και τη στρωματοποίηση των υδάτων. Συγκεκριμένα, στα ανοιχτά της Αλάσκας, η παρουσία των ζώων αυξάνει τις χρονιές που παρατηρούνται όταν η στήλη του νερού είναι πιο θερμή, πιο στρωματοποιημένη, με εντονότερη νότια κυκλοφορία και παρουσία δινών. Επιπλέον διερευνήσεις προτείνουν ότι αυτές οι ωκεανογραφικές συνθήκες αποτελούν χαρακτηριστικά της αποδυνάμωσης του Κυκλώνα της Αλάσκας (Alaska Gyre) και της εισβολής από παράκτιες δίνες μεσαίας κλίμακας, που σχετίζονται με έντονα φαινόμενα El Niño και θερμές φάσεις του Pacific Decadal Oscillation (PDO). Κατά τη διάρκεια των El Niño, τόσο το Υποαρκτικό Μέτωπο (Subarctic Frontal Zone) όσο και η Ζώνη Μετάβασης του Βορείου Ειρηνικού (North Pacific Transition Zone) μετακινούνται βορειότερα μεταφέροντας θηράματα κοντά στον PAPA. Επομένως, είναι πιθανόν η θέρμανση του Ειρηνικού Ωκεανού να προκαλέσει αύξηση της παρουσίας των φυσητήρων στα βόρεια γεωγραφικά πλάτη, συμπεριλαμβανομένου του Κόλπου της Αλάσκας, λόγω της εντατικοποίησης των φαινομένων El Niño που προκαλούν μείωση της διαθεσιμότητας τροφής για αυτούς τους κορυφαίους θηρευτές στους Τροπικούς.

Αυτή η μελέτη είναι η πρώτη που απομονώνει, μελετά και ερμηνεύει με οικολογικούς όρους τη διακύμανση της παρουσίας των φυσητήρων από χρόνο σε χρόνο στο Β. Ειρηνικό. Επίσης για πρώτη φόρα καταγράφεται συστηματικά η παρουσία του είδους στην Ελληνική Τάφρο για όλη τη διάρκεια του έτους, με έμφαση στους χειμερινούς μήνες. Μεθοδολογικά, η χρήση επιτόπου μετρήσεων σε βάθος, η αποικοδόμηση των χρονοσειρών στα στοιχεία τους, και η χρήση σχέσεων χρονικής υστέρησης ανάμεσα στις μεταβλητές απέδωσαν υψηλότερη στατιστική και οικολογική αξία στα αποτελέσματα.

Με τη χρήση των μοντέλων BELLHOP, υπολογίστηκε ότι η απόσταση διάδοσης των ακουστικών σημάτων των φυσητήρων ποικίλει κατά μέσο όρο μεταξύ 7 και 8 km το χειμώνα και το καλοκαίρι αντίστοιχα στο σταθμό PAPA. Οι εποχικές διακυμάνσεις των συνθηκών υποθαλάσσιας διάδοσης του ήχου στο σταθμό

PAPA δεν επηρέασαν τη δυνατότητα ανίχνευσης των ακουστικών σημάτων των φυσητήρων. Στους σταθμούς Άθως και Πύλος, οι αποστάσεις ανίχνευσης ποικίλουν μεταξύ 13 και 22 km, και επηρεάστηκαν από εποχικές διακυμάνσεις των επιπέδων υποθαλάσσιου περιβαλλοντικού θορύβου. Η ταχύτητα του ανέμου συσχετίστηκε με τα επίπεδα θορύβου και στις δυο περιοχές των Ελληνικών θαλασσών σε συχνότητες 3 kHz, ενώ ο θόρυβος από πλοία ήταν επικρατέστερος στην Πύλο κατά τη διάρκεια του καλοκαιριού.

Αξιολόγηση της ικανότητας του ακουστικού καταγραφέα που χρησιμοποιήθηκε να ανιχνεύσει φυσητήρες έδειξε ότι ο Παθητικός Υδροκαταγραφέας (PAL) είναι ένα οικονομικό και ιδιαίτερα αποδοτικό εργαλείο για να ανιχνεύει τα ακουστικά επικρατέστερα είδη κητωδών σε κάθε περιοχή. Για την ανίχνευση διαφορετικών ή επιπλέον ειδών χρειάζονται προσαρμογές στα κριτήρια δειγματοληψίας και στον αυτόματο ανιχνευτή του οργάνου. Παρέχονται προτάσεις για ειδικές τροποποιήσεις του αλγόριθμου ώστε να αυξηθεί η ανιχνευσιμότητα των ειδών προς παρακολούθηση σε διαφορετικά ηχοτοπία. Μειωμένη διακύμανση του αριθμού των φυσητήρων που καταγράφηκαν στην Αλάσκα έδειξε ότι η πιθανότητα ανίχνευσης τους ξεπερνά το 50% καθ’ όλη τη διάρκεια του έτους. Παρόλα αυτά, στη Πύλο, μια μείωση στη διάρκεια των ηχητικών αρχείων κατά τους εννιά πρώτους μήνες, είχε αρνητική επίδραση στη πιθανότητα ανίχνευσης των «κλικ» από φυσητήρες και πιθανόν προκάλεσε την υποτίμηση της ακουστικής παρουσίας τους στη περιοχή. Επομένως, είναι πολύ πιθανό η πραγαμτική παρουσία των φυσητήρων στην Ελληνική Τάφρο να είναι πολύ πιο συχνή και έντονη από ότι καταγράψαμε.

Επιπλέον, αυτή η διατριβή παρέχει ουσιαστική πληροφορία βάσης για τα επίπεδα περιβαλλοντικού θορύβου σε όλες τις περιοχές μελέτης, και ενισχύει τις ανησυχίες σχετικά με τα υψηλά επίπεδα θορύβου στη Πύλο. Η περιοχή της Ελληνικής Τάφρου αποδείχτηκε η πιο θορυβώδης, με περίπου 10 και 12 dB διαφορά στις χαμηλές συχνότητες, κατά τη καλοκαρίνη περίοδο. Ο θόρυβος αυτός σχετίζεται με την έντονη κίνηση των πλοίων. Ο Σταθμός της Πύλου βρίσκεται πάνω σε μια κεντρική γραμμή κίνησης μεγάλων πλοίων και τάνκερς. Επομένως, τόσο οι φυσητήρες όσο και η υπόλοιπη κητοπανίδα που διαβιεί στην Ελληνική Τάφρο είναι εκτεθειμένοι σε υψηλότερο κίνδυνο ενόχλησης από ανθρωπογενή θόρυβο, αλλά και σύγκρουσης με πλοία.

Συνολικά, αυτή η διατριβή αποκαλύπτει εποχικά μοτίβα διακύμανσης της παρουσίας των φυσητήρων στα ανοιχτά του Κόλπου της Αλάσκας και στο Ιόνιο Πέλαγος, και επιχειρεί να εξηγήσει τις διαδικασίες που τα επηρεάζουν. Ακόμα, μέσα από τα αποτελέσματα αυτής της εργασίας δίνεται έμφαση στη χρησιμότητα των μακροχρόνιων ακουστικών δεδομένων για τη βελτίωση της επιστημονικής γνώσης σχετικά με την οικολογία των φυσητήρων. Απώτερος στόχος της παρούσας εργασίας είναι να συμβάλει στις προσπάθειες προστασίας και διατήρησης του είδους στις ευρύτερες περιοχές μελέτης. Συγκεκριμένα, η Ελληνική Τάφρος είναι μια περιοχή με ιδιαίτερο διαχειριστικό ενδιαφέρον καθώς ο μικρός πληθυσμός των φυστήρων εκεί απειλείται όχι μόνο από το θόρυβο και το ρίσκο σύγκρουσης με πλοία αλλά και από τα σχέδια της Ελληνικής Κυβερνησης για αναζήτηση και εξόρυξη υδρογονανθράκων. Αυτές οι συνθήκες υποβαθμίζουν το σημαντικό αυτό ενδιαίτημα για το είδος. Η ACCOBAMS, η Συνθήκη για τη Διατήρηση των Κητωδών στη Μεσόγειο, εχει πρόσφατα ανακυρήξει την Ελληνική Τάφρο ως σημαντική περιοχή για τα θαλασσια θηλαστικά (IMMA: Important Marine Mammal Area) με στόχο να θεσπιστεί νομικά ως Θαλάσσια Προστατευόμενη Περιοχή. Οσον αφορά στο σταθμο PAPA, το Αμερικάνικο Ναυτικό διατηρεί μια περιοχή οπου εκτελούνται ασκήσεις που συμπεριλαμβάνουν χρήση σόναρ και εκρηκτικών στα ανοιχτά της Αλάσκας Τέτοιες δραστηριότητες μπορεί να αποτελέσουν απειλή για την ευημερία των ζωων που διαβιουν στην ευρυτερη περιοχή.

Και οι τρεις περιοχές μελέτης αποδείχθηκαν πλούσιες σε κητοπανίδα, ενώ η Πυλός και η PAPA αποτελούν σηματικούς βιότοπους για τους τοπικούς πληθυσμούς φυσητήρων. Για να εμπλουτίσουμε τη γνώση μας σχετικά με την οικολόγία των φυσητήρων και γενικά των κητωδών, αλλα και για να αξιολόγησουμε τις ενδεχόμενες επιπτώσεις από τη κλιματική αλλαγή, χρειάζεται να αυξηθούν οι ακουστικοί σταθμοί ώστε να αποκτήσουμε δεδομένα με καλύτερη γεωγραφική κάλυψη, και να διευρυνθεί η διάρκεια των δειγματοληψιών, τόσο στον Ειρηνικό Ωκεανό όσο και στη Μεσόγειο Θάλασσα.

Epigraph

Σα βγεις στον πηγαιμό για την Ιθάκη,
να εύχεσαι νάναι μακρύς ο δρόμος,
γεμάτος περιπέτειες, γεμάτος γνώσεις.
Τους Λαιστρυγόνας και τους Κύκλωπας,
τον θυμωμένο Ποσειδώνα μη φοβάσαι,
τέτοια στον δρόμο σου ποτέ σου δεν θα βρεις,
αν μέν’ η σκέψις σου υψηλή, αν εκλεκτή
συγκίνησις το πνεύμα και το σώμα σου
αγγίζει.
Τους Λαιστρυγόνας και τους Κύκλωπας,
τον άγριο Ποσειδώνα δεν θα συναντήσεις,
αν δεν τους κουβανείς μες στην ψυχή σου,
αν η ψυχή σου δεν τους στήνει εμπρός σου.

Να εύχεσαι νάναι μακρύς ο δρόμος.
Πολλά τα καλοκαιρινά πρωιά να είναι
που με τι ευχαρίστησι, με τι χαρά
θα μπαίνεις σε λιμένας πρωτοειδωμένους·
να σταματήσεις σ’ εμπορεία Φοινικικά,
και τες καλές πραγμάτειες ν’ αποκτήσεις,
σεντέφια και κοράλλια, κεχριμπάρια κ’
έβενους, και ηδονικά μυρωδικά κάθε λογής,
όσο μπορείς πιο άφθονα ηδονικά μυρωδικά·
σε πόλεις Αιγυπτιακές πολλές να πας,
να μάθεις και να μάθεις απ’ τους
σπουδασμένους.

Πάντα στον νου σου νάχεις την Ιθάκη.
Το φθάσιμον εκεί είν’ ο προορισμός σου.
Αλλά μη βιάζεις το ταξίδι διόλου.
Καλλίτερα χρόνια πολλά να διαρκέσει·
και γέρος πια ν’ αράξεις στο νησί,
πλούσιος με όσα κέρδισες στον δρόμο,
μη προσδοκώντας πλούτη να σε δώσει η
Ιθάκη.
Η Ιθάκη σ’ έδωσε τ’ ωραίο ταξίδι.
Χωρίς αυτήν δεν θάβγαινες στον δρόμο.
Άλλα δεν έχει να σε δώσει πια.
Κι αν πτωχική την βρεις, η Ιθάκη δεν σε
γέλασε.
Έτσι σοφός που έγινες, με τόση πείρα,
ήδη θα το κατάλαβες οι Ιθάκες τι σημαίνουν.

Ιθάκη

- **Κ.Π. Καβάφης**

As you set out for Ithaka
hope the voyage is a long one,
full of adventure, full of discovery.
Laistrygonians and Cyclops,
angry Poseidon—don’t be afraid of them:
you’ll never find things like that on your way
as long as you keep your thoughts raised high,
as long as a rare excitement
stirs your spirit and your body.
Laistrygonians and Cyclops,
wild Poseidon—you won’t encounter them
unless you bring them along inside your soul,
unless your soul sets them up in front of you.
Hope the voyage is a long one.
May there be many a summer morning when,
with what pleasure, what joy,
you come into harbors seen for the first time;
may you stop at Phoenician trading stations
to buy fine things,
mother of pearl and coral, amber and ebony,
sensual perfume of every kind—
as many sensual perfumes as you can;
and may you visit many Egyptian cities
to gather stores of knowledge from their scholars.
Keep Ithaka always in your mind.
Arriving there is what you are destined for.
But do not hurry the journey at all.
Better if it lasts for years,
so you are old by the time you reach the sland,
wealthy with all you have gained on the way,
not expecting Ithaka to make you rich.
Ithaka gave you the marvelous journey.
Without her you would not have set out.
She has nothing left to give you now.
And if you find her poor, Ithaka won’t have fooled
you.
Wise as you will have become, so full of
experience,
you will have understood by then what these
Ithakas mean.

Ithaka

- **C. P Cavafy**

1. General Introduction

As for me, I am tormented with an everlasting itch for things remote. I love to sail forbidden seas, and land on barbarous coasts.

— Herman Melville, Moby-Dick or, The Whale

Oceans worldwide are experiencing alterations of their complex patterns of biodiversity due to climate change (Gitay et al., 2002). Major effects of these alterations on species and ecosystems include but are not limited to: shifts in distribution patterns; effects on reproduction and survival rates; extinction or extirpation of isolated populations/species; reductions in population size; habitat loss, fragmentation or degradation; increased spread of parasites and frequency of toxic blooms; introduction and increase of invasive species (Gitay et al., 2002; Cheung et al., 2009; Mawdsley et al., 2009). With environmental conditions influencing the habitat selection of animals, climate fluctuations are a factor with significant contribution to the future distribution and survival of organisms, populations, or entire species. In the context of global change, species abundance and distribution have a dual role and significance. Initially, disruptions in patterns of biodiversity can be recognized as ecological responses to oceans' warming and be used as indications of a changing environment. In this case, shifts in biodiversity are perceived as the initiation of cascade effects on trophic levels and human societies. These ecological consequences can alter the community structure of marine ecosystems; interfere with the conservation of endangered species; prevent sustaining marine ecosystem functions and services. These are coupled with concomitant socio-economic consequences for commercial fisheries, the whale-watching industry, and a plethora of anthropogenic activities. At the same time, biodiversity can be seen as the safeguard against the effects of global warming perturbations. Marine and terrestrial ecosystems characterized by larger number of species are expected, due to their higher functionality and productivity, to be more resilient and less vulnerable in the face of changing environments (Loreau, 2001). Ranging from the Mediterranean forests with mixed tree species to the tropical reefs with an abundance of coral and fish species, high-diversity regions enhance ecosystem productivity and are more resilient and adaptable in the face of abiotic and biotic stressors (Bellwood and Hughes, 2001; Riofrío et al., 2017). However, these highly functional communities are becoming increasingly scarce.

As human population increases, the possibility of an overlap between human activities and marine wildlife becomes alarmingly high. Since habitat usually declines when human activity increases, the impact of anthropogenic presence on marine ecosystems tends to be negative. Climate change effects upon ecosystem health are expected to have synergistic interactions with a variety of anthropogenic activities and further challenge our ability to conserve biodiversity (Lotze and Worm, 2002; Worm et al., 2002). Ocean warming, sea level rise, salinity shifts and oxygen reduction reflect environmental changes caused by climate change. Overfishing and depletion of prey resources, chemical pollution, habitat degradation, and increasing underwater manmade noise are only a few by-products of human activities in the marine environment that raise conservation concerns for its communities. The evidence until now suggests that distribution patterns and abundance of marine organisms will shift in response to the alterations in the ocean conditions caused by direct or indirect human interference (Hazen et al., 2012).

To attempt predictions of human impact on the distribution patterns of marine biodiversity, in particular of specific populations and species, a prerequisite is to provide baseline information on the status and distribution of biodiversity. A major challenge that scientists face while investigating long-term changes of biodiversity (mainly when examining climate change effects) is the requirement of long-term data sets. The observational record, especially when it refers to mobile marine organisms, is typically of a very patchy nature with large discontinuities in species distribution data in both spatial and temporal scales. Since patterns of biodiversity vary by species, latitude, habitat type, region, and time, the knowledge of 'who is where and when' becomes important. The answers to 'where' and 'when' are related to questions related to a species' habitat use. Every species has different physical and biological requirements, known as habitat preferences. The examination of these habitat preferences refers to the 'why' and is ecologically essential for distribution studies. Therefore, current or past spatiotemporal occurrence patterns of species in the long-term and their relationship to environmental conditions need to be understood in order to predict the future of biodiversity and the health of oceanic systems. Overall, an improved understanding of species' ecology is required, and that is the broader focus of this dissertation. Currently, most of the research implemented on biodiversity globally is limited to certain taxa, and focuses on coastal and continental shelf regions (Beaugrand et al., 2002; Hoegh-Guldberg et al., 2007). Relatively little is known about the open oceans, the offshore and deep-water pelagic systems, and large data gaps remain in the distribution of deep-sea life and deep-diving cetaceans (Whitehead et al., 2008; Tittensor et al., 2010).

The study of marine apex predators is an effective way to track environmental shifts in the oceans (Bossart, 2006). Monitoring the distribution of top predators can provide indications for the distribution and abundance of their prey populations, and an evaluation of the status of their habitat and entire ecosystem (Piatt and Springer, 2007; Moore and Huntington, 2008). The knowledge and understanding of preferred habitat characteristics of top predators can be invaluable in understanding changes in the oceanic conditions based on the marine top predator distributional responses (Forney, 2000). The foundation of this concept is a bottom-up approach of ecosystem responses and can be used to alert us in order to mitigate potential negative trends in the health of the ecosystems. Eventually, such information is crucial for identifying critical habitats for marine wildlife and ultimately informing conservation efforts. The establishment of sites for marine protected areas is based on the habitat-use and habitat-preference studies of marine top predators. For these reasons, certain apex marine predators, and specifically marine mammals, are recognized as ecosystem sentinels (Bossart, 2006). Relatively recent examples highlight the role of marine mammals in warning us of the effects of changing oceans. Firstly, the unusual mortality event of California sea lion pups (*Zalophus californianus*) in Southern California between 2013-2017. Anomalously increased numbers of dead or emaciated sea lion pups was related to a strong El Niño event, which caused an anomalous increase in water temperature (Elorriaga-Verplancken et al., 2016). The higher than usual water temperatures were associated with a primary productivity decline in the coastal zone, which increased foraging in the oceanic offshore habitats causing also the foraging effort of sea lions to rise (Elorriaga-Verplancken et al., 2016). Around the same period, in early 2016, the largest sperm whale stranding event reported in the North Sea involved 30 immature males stranded in five countries over six weeks. Nine out of the 30 individuals stranded were found to have ingested marine litter (IJsseldijk et al., 2018). Even though the litter did not appear to have caused the stranding of the whales, and the exact causes of the strandings remain uncertain, it provides evidence of the extent to which human activities can negatively affect the not-so-distant oceanic life and our ability to track those impacts through the study of marine mammals.

1.1 Study Species: The Sperm Whale

Odontocetes (often referred to as toothed whales), and specifically sperm whales (*Physeter macrocephalus*), are apex predators. Among the 73 species of odontocetes in the world, sperm whales are the largest. They also hold the record of possessing the largest brain on Earth (Kojima, 1951), speculated to be related mostly with a social intelligence function (Whitehead, 2003). They exhibit large behavioral and physical sexual dimorphism, with males having three times the mass of females (Whitehead, 2003). Mature males, in the North Pacific, are larger than 15 m long, weigh up to 45 tons, while adult females are about 11 m long, and weigh up to 15 tons. However, the Mediterranean population appears to be smaller, likely due to their exposure to limited resources. Specifically, for the entire Mediterranean Sea, Drouot et al. (2001) estimated the sperm whale maximum size at 13.5 m, while in the Ionian Sea males' maximum length was estimated at 14.6 m and 9.5 m for females (Frantzis and Alexiadou, 2008a; Frantzis, Alexiadou, et al., 2014; Caruso et al., 2015). The life span of sperm whales is between 70-100 years, with females maturing at ages 7–13 yr, and males maturing between the ages of 18–21 yr (Rice, 1989). Females bare a single calf at a time. Calves are often provided alloparental care both during the mothers' deep foraging dives to protect from predators and for suckling (Gordon, 1987; Whitehead, 2003).

The behavioral dimorphism in this species refers mainly to the complex structure of the sperm whale communities, where mature males and females are not typically sympatric year-round. Females with the young form stable social units, the 'social groups', and live year-round in lower latitudes and temperate waters. Young males leave their social groups at an age of around 3-15 years old and form loose associations with other young males; the so-called ‘bachelor schools’ travel to higher latitudes during the summers to forage (Best, 1979). Older males tend to be more solitary, migrating to high latitudes during the warm season when prey abundance increases, and usually returning to low latitudes to breed in the winter (Best, 1979). Both in the Mediterranean and in the Pacific, sperm whales have a typical home range around 1000 km (Whitehead, 2003; Rendell et al., 2014).

Sperm whales have a wide geographical distribution, are found throughout the world’s oceans, from the equator to the edges of both polar pack-ice zones (Whitehead, 2003). Currently, about 360.000 are estimated to exist worldwide, which is only 32% of the population during the pre-whaling era (Whitehead, 2002). Even though whaling dramatically reduced their numbers, sperm whales remain important oceanic predators and consume about 100 megatons of biomass per year (Whitehead, 2003). In most parts of the world, they feed primarily on cephalopods. They have evolved to extremely efficient meso- and bathy-pelagic squid predators. In the North Atlantic, North Pacific and New Zealand, fish makes a substantial part of the sperm whale diet, and mostly that of the males (Kawakami, 1980). In order to maintain their large size, sperm whales eat about 350-750 squid daily, which requires that they spend most of their time deep in the oceans (Best, 1999; Whitehead, 2003). Notorious for their deep-diving abilities, they can go down to a depth of 2 km in pursuit of their prey. They typically dive 400 to 900 m for 30 to 50 min at a time with spending approximately 10 min intervals at the surface between dives (Jaquet and Gendron, 2002; Amano and Yoshioka, 2003; Watwood et al., 2006). These extended dive periods make observation difficult, especially in the open ocean under rough weather conditions and particularly during the nighttime.

Like all cetaceans, sperm whales have evolved to adjust perfectly to the darkness of the ocean. Underwater, visibility is limited to the upper 100 to 200 m of ocean depth, so the propagation of sound is favored over light (Urick, 1983). As a result, all cetaceans have developed effective systems of producing and receiving sounds in order to interact with one another and their environment (Tyack, 2000). Vocalizations vary among species according to their physical characteristics, with frequencies ranging from 10Hz to 250 KHz. These sounds can be instinctive, genetically programmed, or learned through others via social learning: vertically (from parents to offspring), obliquely (from the previous generation via a nonparent model to younger individuals), or horizontally (between unrelated individuals from similar age classes or within generations).

Sperm whales are capable of producing sound from when they are born (Madsen et al., 2003) and can make clicks consistent with echolocation while they dive down to a maximum 662 m depth for as long as 44 min, within only the first year of their life (Tønnesen, 2018). Sperm whales use almost 1/3 of their body as a massive sound-producing organ, which produces clicks with the highest source levels of a biologically-produced sound recorded (Madsen, Payne, et al., 2002). A liquid waxy substance occupies 40% of the animal's head, the spermaceti organ, which functions as an amplifier for the clicks. Each click they produce consists of a number of periodical pulses that are the result of multiple reflections of the original sound in the animal's head (Norris and Harvey, 1972). The distance between two successive pulses, called Inter-Pulse Interval (IPI), is related to the time it takes a pulse to travel twice along the spermaceti organ, and is associated to the size of the animal (Gordon, 1991). The spaces between two successive clicks, called Inter-Click Interval (ICI), characterize different patterns and types of vocalizations that have been attributed to certain functions. Among the most common sperm whales calls: the ‘usual’ clicks, the ‘codas, the ‘slow’ clicks, and the ‘creaks’. Sperm whales also produce “gunshots”, non-click vocalizations, and lower intensity sounds such as “trumpets”, “short trumpets”, “chirrups”, “squeals”, “pips” and “moans” that are less frequent (Goold, 1999).

Function of the main sperm whale click patterns have been extensively studied and are largely understood, for which there is a consensus among researchers. The usual clicks and creaks are short, directional signals involved in long-range and short-range active echolocation on prey, respectively. Creaks are indication of feeding events, and thus may also be used by eavesdropping whales as a reliable signal of feeding behavior. Codas have irregular ICI, are less directional and are produced by females and immature males during social interactions (Whitehead and Weilgart, 1991). Communication seems to be the codas’ main role and a geographical and cultural variation exists in coda types (Pavan et al., 2000; Rendell and Whitehead, 2003; Gero, Bøttcher, et al., 2016). Slow clicks are produced by males, are longer in duration, exhibit large ICI, with emphasis on low frequency and low directionality, suggesting a long distance communication-related function, likely associated with competition for food and/or for mates in the breeding grounds (Weilgart and Whitehead, 1988). Part of the behavioral sexual dimorphism in sperm whales refers to the acoustic repertoire of solitary males that perform few social interactions at high latitudes and differs from the social groups in the tropics by the lack of coda exchanges (Weilgart and Whitehead, 1988; Madsen, Wahlberg, et al., 2002). The variation among sperm whale vocalizations has been used to investigate many parts of the sperm whales’ behavior and population ecology.

1.2 Passive Acoustic Monitoring

The recording and analysis of sperm whale (or any other species) sounds to investigate their ecology falls into the discipline of 'acoustic ecology'. Specifically, acoustic ecology is defined as the study of the relationship, mediated through sound, between living beings and their environment. Important keywords within this discipline include 'soundscapes', 'ambient noise levels', 'detection range', 'bioacoustics', 'oceanographic properties', 'detection probability', 'Passive Acoustic Monitoring' (PAM) and many others. Bioacousticians, acoustic ecologists, and this dissertation are concerned with questions such as: Which cetacean species can my acoustic recorder detect? Are there any temporal patterns in the detection of these species? What are the environmental conditions that drive those patterns? Do changes in the water properties affect the detectability of the animals? How far away are the animals that I detected? Do underwater background noise levels change in time and space, and can they obscure the sounds of the whales I wish to record?

The technology developed to study marine soundscapes is based on hydrophones; these are underwater microphones that record sound in the oceans. The use of hydrophones and the availability of long-term passive acoustic recordings first became possible during World War I (Lemon, 2004) and since then have provided scientists with a better understanding of the distribution and temporal variability in cetacean occurrence around the world (Mellinger et al., 2007). Today, there is a variety of acoustic equipment used to record sperm whales and other cetacean vocalizations: towed hydrophone arrays (e.g., Russell Leaper et al., 2000); seafloor and buoy mounted autonomous recorders (e.g., Mellinger et al., 2004; Fournet et al., 2018);

cabled seafloor arrays (e.g., Caruso et al., 2015); sonobuoys (e.g., Dunn, 1969); gliders and other autonomous acoustic vehicles (e.g., Klinck et al., 2012; Mellinger et al., 2012); and animal-borne tags (Fregosi et al., 2016; Tønnesen, 2018). Different tools can provide either continuous recordings or short acoustic files sampled under a predefined duty cycle. Depending on the research question and the amount of data available, analysts either manually inspect waveforms and spectrograms of the recordings (Mellinger and Clark, 2000) or use automatic detection algorithms (i.e. the software packages Osprey, Mellinger 1995; Ishmael, Mellinger 2002; or Triton, Wiggins et al. 2010). The use of automated detectors has the advantage of unbiased assessment; or rather introduces a consistent bias that does not change depending on the analyst or the data set. More importantly, automated methods are essential when analyzing continuous recordings from many years and many different stations. However, a number of existing automated detectors have a high rate of false detections. Most of the bioacousticians that use them are often required to check the detections manually after the detector runs. Increased noise levels, overlapping acoustic signals by multiple animals, calls with lower signal-to-noise-ratio, and detections of atypical types of vocalizations, are common reasons that automated detectors miss detections of the signals of interest.

The recordings, once the targeted signals are detected and classified, can help answer a suite of scientific questions. A great deal of bioacoustics research has been implemented around the world, based on the sperm whale's exceptional vocal capabilities. Worthington and Schevill (1957) were the first to scientifically describe the sperm whales' clicks and in a more thorough investigation, Backus and Schevill (1966) reported their characteristics. The nature of the sperm whale's clicks and their characteristics have been investigated by Møhl et al. (2000, 2003) and Goold and Jones (1995) off Norway and off the Azores, respectively. Long-term studies of both diving and surface acoustic behavior have been conducted on female and immature whales off the Galapagos Islands (Whitehead and Weilgart, 1991), off Sri Lanka (Gordon, 1987), off northern Norway (Madsen, Payne, et al., 2002; Wahlberg 2002), and on male sperm whales off Kaikoura, New Zealand (Jaquet et al., 2000, 2001). In the Mediterranean Sea, Pavan et al. (2000) described coda patterns recorded over 10 years of field work, Frantzis and Alexiadou (2008) studied the coda occurrence and types produced by males, Teloni and Alle (2005) described their acoustic behavior during three years of surveys, and both Pirotta et al. (2011) and Frantzis et al. (2014) quantified the sperm whale habitat preferences. Around the Galapagos Islands and at the Caribbean Sea, Rendell and Whitehead (2004) and Gero et al. (2015, 2016) investigated the coda characteristics in order to attribute to them dialect/cultural functions and examine social structure. Tag data has been used to study the vocal and diving behavior of adults and calves (Watwood et al., 2006; Tønnesen, 2018) and the structure of clicks and sound production (Madsen, Payne, et al., 2002). Additional bioacoustic studies focused on the localization (Thode, 2004; Laplanche et al., 2005) and length estimation of individuals (Rhinelander and Dawson, 2004; Mathias et al., 2009); abundance and density estimation (Drouot et al., 2001; Barlow and Taylor, 2005); spatiotemporal distribution patterns in the North Pacific, the North Atlantic, and the Mediterranean Sea (Mellinger et al., 2004; Pirotta et al., 2011; Wong and Whitehead, 2014; Stanistreet et al., 2018).

PAM methods have developed greatly over the last few decades (Mellinger et al., 2007). The advancement and wider availability of autonomous passive acoustic technology has allowed us to acquire cetacean recordings in more remote locations, for longer periods of time and irrespective of light and weather conditions, at a relatively low cost and in a non-invasive manner. Additional benefits of PAM include the coverage of a larger area (10-37 km) compared to visual methods, which increases the number of whales detected, particularly the deep divers such as sperm whales, by more than five times (Barlow and Taylor, 2005; Mathias et al., 2013).

Some limitations occur naturally with the use of passive acoustic methods. Even though most (if not all) cetacean species are vocal and can be acoustically detected, there are still occasions that the animals may be acoustically inactive. For example, Barlow and Taylor (2005) encountered a group of sperm whales in the North Pacific that remained silent for three hours. For sperm whales, this represents a rather uncommon vocal behavior. Despite the extensive work on characterizing vocalizations by a large number of cetacean species, acoustic signals produced by certain odontocetes, mainly dolphins, remain difficult to classify into species level (Oswald, 2003). Challenges during acoustic data analyses include the detection of unknown sounds. With the absence of visual confirmation, the interpretation and classification of these sounds may be no more than speculative. Additionally, assessment of gender, diurnal variability in vocal behavior, or group size, although possible in some cases with the use of continuous recordings and multiple sensors, is still challenging and limited. At the same time, the acquiring of long-term continuous acoustic recordings at high sampling rates (necessary for odontocetes) requires storage considerations to be made, for acoustic data sets are of an exceptionally large volume. On the other hand, the use of non-continuous recordings, which results in a sampling strategy based on certain duty cycle, may introduce biases to the temporal patterns examined and the cetacean diversity investigated. The probability of detecting an acoustical signal depends on a combination of factors such as the amplitude, acoustic behavior and the vocalization rate of the source; the sound propagation conditions determined by the acoustic characteristics of the calls, and environmental conditions (water density, bathymetry etc.); and the ambient sound levels. For example, acoustic signals of lower frequency propagate further, while higher noise levels tend to decrease the range that calls can be detected. Investigations of the marine biological soundscapes should include considerations of these variables. For these reasons, acoustic data analysis can be complex. Nonetheless, PAM provides a unique opportunity to fill the critical knowledge gap regarding the temporal patterns of sperm whales in offshore locations and their habitat preferences, which is the focus of this dissertation.

1.3 An Ocean & the Sea

The data presented here were collected in three different regions and mainly two different bodies of water. The geographic scope of my study includes an open-ocean location in the offshore Gulf of Alaska in the Northeast Pacific Ocean, and two offshore deep sites in the Greek Seas, in the Eastern Mediterranean Sea. When we compare the largest of all the oceans to a semi-enclosed sea, an ecological study might seem almost meaningless. However, even if the Pacific Ocean is 46% of the Earth's water surface and the Mediterranean is just 0.82%, disproportionally high biodiversity and endemism characterize the Mediterranean marine ecosystem with its fauna and flora representing 7% of the described macroscopic species (Bianchi and Morri, 2000). This remains particularly surprising, considering the extreme oligotrophy (due to the poor nutrient supply) of the Mediterranean. In fact, as one moves east into the Mediterranean basin, the oligotrophy is accentuated and productivity decreases (Dugdale and Wilkerson, 1988). At the same time, the major circulation gyre of the North Pacific, the North Pacific Subtropical Gyre, is also referred to as oligotrophic. With bottom depths that exceed 5000 m, rich and diverse biota, and a complex combination of physical, chemical, climatic and environmental characteristics, the Mediterranean Sea is described as a ‘miniature ocean’ (Bethoux et al., 1999).

Despite the large ecological asymmetries between the two regions, they are both inhabited by a large apex predator, the sperm whale (Mellinger et al., 2004; Rendell and Frantzis, 2016). Variation in environmental conditions and human activities can result in varying ecological patterns at the marine ecosystem. A long history of extensive whaling and increasing extreme El Niño–Southern Oscillation (ENSO) events in the Pacific Ocean, and the intense shipping traffic and dramatic interactions with fishing gear in the Mediterranean Sea, can be devastating to marine fauna and likely sperm whale populations (Barber and Chavez, 1983; Cai et al., 2014; Notarbartolo di Sciara et al., 2016). Thus, Mediterranean sperm whales are expected to be subject to different ecological forces and human pressures than those experienced by their North Pacific counterparts. Based on these differences and the similarities between the North Pacific and the Mediterranean Sea, the study sites were chosen to investigate the temporal patterns and the ecology of geographically and genetically separated populations of the same species.

1.4 The Greek Seas, Northeast Mediterranean Sea

The low nutrient reserves that drive low levels of primary productivity in the East Mediterranean basin, contrast the relatively high fisheries production

(Papaconstantinou and Farrugio, 2000). The so-called "Mediterranean paradox" can be explained by the importance of nutrient supply from the atmosphere and land runoff, and the contribution of localized hydrographic structures such as mesoscale eddies, frontal zones and small scale upwellings (Papaconstantinou and Farrugio, 2000; Boero, 2015). Despite this oligotrophy, twelve cetacean species have been recorded in the Greek Seas, with seven of them frequently encountered (Frantzis et al., 2003). Among them, the common dolphin (*Delphinus delphis*), harbor porpoise (*Phocoena phocoena*) and the sperm whale are listed as Endangered under the criteria of the International Union for the Conservation of Nature.

The first studies on cetaceans in Greece began more than 2360 years ago. Aristotle was the first to study and record dolphins (from Greek δελφύς (*delphus*), "womb" and referred to "a 'fish' with a womb") and their acoustic behavior. In the 'Των περί τα ζώα Ιστοριών' (*Historia Animalium*), Aristotle claimed that dolphins were mammals: he observed that they bore their young alive and suckled them, breathed air and communicated by underwater sounds. He even used a basic form of photo-identification and tagging methods to conduct his research. In his writings, we also find descriptions of sperm whales. It is hypothesized that his sightings originate from the North Aegean Sea, since he was born on the Chalkidiki Peninsula (Rendell and Frantzis, 2016). Today, genetic analysis results support that the sperm whales encountered in the Mediterranean Sea do not regularly move to the Atlantic Ocean, indicating genetic and geographic isolation (Engelhaupt et al., 2009). Bioacoustics analysis verifies this separation showing a distinction of the codas that the Mediterranean whales produce. One only coda type, the '3+1', dominates all recordings within the entire basin, and can be used as additional evidence of population structure and vocal culture (Pavan et al., 2000; Rendell and Whitehead, 2003; Frantzis and Alexiadou, 2008a; Rendell et al., 2012). On the other hand, intra-basin movements to and from the eastern and western Mediterranean have been reported for males (Rendell and Frantzis, 2016). In contrast to the oceanic populations, here, solitary males, bachelor schools and social groups are not geographically segregated. Even though in the western Mediterranean basin, more solitary animals are encountered in the northern areas and more groups with calves are encountered in the southern areas (Drouot et al., 2004), in the Greek Seas and other parts of the Mediterranean all social classes inhabit the same waters (Pirotta et al., 2011; Frantzis, Alexiadou, et al., 2014). Their typical displacements are estimated around 400 to 600 km across a period of one year (Rendell et al., 2014).

The Hellenic Trench is one of the areas in the Mediterranean with the highest sperm whale density (Gannier et al., 2002; Boisseau et al., 2010). Here, most of the animals are encountered at the 1000-m depth contour (Frantzis, Alexiadou, et al., 2014). Habitat preference studies in the western basin indicate that the continental shelf edge, lower sea surface temperatures, and higher chlorophyll are conditions associated with higher sperm whale presence (Praca and Gannier, 2008a; Pirotta et al., 2011).

The Greek Seas are inundated with human activities disrupting to marine wildlife. Despite the absence of any whaling within the Mediterranean basin, concerns about the conservation of the local sperm whale population are increasing. With about 30% of the global commercial shipping, and 20% of the world's oil shipping passing through the Mediterranean Sea, shipping traffic consists among the most important interference to the cetacean fauna in the area. For the International Maritime Organization to assist in protection efforts and make alterations in shipping lanes, and/or speed limits in critical sperm whale habitats, solid evidence of the year-round sperm whale presence is a prerequisite (Rendell and Frantzis, 2016). Despite all the technological advancements in cetacean observation, large knowledge gaps still remain for the sperm whale (and other cetacean species) distribution patterns in the entire eastern Mediterranean basin, including the Greek Seas (Mannocci et al., 2018). Although important, but limited, research effort has been implemented in the west coast of Greece (Ionian Sea), the Aegean Sea is the least surveyed part of the Mediterranean (Notarbartolo di Sciara et al., 2016; Mannocci et al., 2018). Overall, the need for cetacean information during seasons other than summer, for all sites of the Greek Seas, persists today.

1.5 The Gulf of Alaska, Northeast Pacific Ocean

Coastal waters of the Gulf of Alaska (GOA) are highly productive (Denman et al., 1981), supporting rich fisheries and a variety of cetacean species, with a minimum of 15 species that occur either seasonally or year-round (Rone et al., 2017). The continental shelf waters are rich in iron which is supplied by processes such as coastal upwelling, river discharge, tidal mixing, and estuarine circulation (Chase et al., 2002). Whereas, the oceanic waters are iron-limited and much less productive (Boyd et al., 1996). Processes that allow transport of nutrient-rich water from the coastal zone to the offshore region can enhance phytoplankton growth and productivity in the pelagic ecosystem of the GOA (Whitney, Crawford, and Harrison, 2005). The North Pacific Subarctic Gyre (also known as the Alaska Gyre) and the Alaska Current dominate the general circulation and oceanography in the GOA and do not typically create the conditions for offshore nutrient transport. Mesoscale eddies and gyre recirculation events can export large volumes of iron-rich water into the open ocean at more than 1000 m depth (Whitney, Crawford, and Harrison, 2005). The GOA oceanographic conditions, both on the coastal and the oceanic habitat, fluctuate over time and are influenced by climate variability, both ENSO events (Whitney et al., 1998) and decadal oscillations (Combes and Di Lorenzo, 2007). Strong El Niño events and shifts in the Pacific Decadal Oscillation (PDO) regime impact the intensity of mesoscale eddies and the gyre recirculation in the GOA, affecting in this way the productivity of the offshore ecosystems (Stabeno et al., 2004).

Cetaceans encountered in the complex ecosystem of the GOA range from small-sized coastal species such as: the harbor porpoise (*Phocoena phocoena*) to the largest pelagic mysticetes such as: the blue whale (*Balaenoptera musculus*) and deep-diving odontocetes like sperm whales (Mellinger et al., 2004; Rone et al., 2017). Among the 15 species present in the GOA, seven cetaceans including the sperm whale are listed as Endangered in the United States (US) under the Endangered Species Act (ESA) of 1973. The eastern North Pacific sperm whales are currently divided, for US management purposes, into three stocks: the Alaska, the California/Oregon/Washington, and the Hawaii stock (Allen and Angliss, 2013). However, extensive meta-analysis of whaling data provided no indication of separate stocks in the pelagic North Pacific (Mizroch and Rice, 2013). Nonetheless, the segregation of age and sex classes is recognized in the Pacific, with the social units of females and calves dominating the tropics, while solitary males and bachelor schools spend summers in the subarctic (Whitehead, 2003). However, Mizroch and Rice (2013) confirm that females were found in waters north of 50^0N, suggesting that matrilineal groups are likely to inhabit offshore Alaskan waters today especially in the most productive areas. In contrast to baleen whales, annual migration patterns are not established for sperm whales. The social structure and the behavioral dimorphism in sperm whale societies are not based on annual migration patterns but in year-round presence of the different groups, males and females with young, in the high and low latitudes respectively.

Whaling records have provided most knowledge of sperm whale distribution in offshore areas throughout the GOA (Berzin and Rovnin, 1966; Ivashchenko et al., 2014; Clapham and Ivashchenko, 2016). Based on Yankee whaling charts, few sperm whales were caught in the offshore GOA mainly during May, July and August, while large aggregations of whales were found on the Equator (Mizroch and Rice, 2013). Modern pelagic whaling data showed a relatively high concentration of sperm whales off the Washington coast, and Mizroch and Rice (2013) suggest a possible division between a coastal and a pelagic stock of sperm whales in the Northeast Pacific. Even though Mellinger et al. (2004) reported a seasonal pattern based on the acoustic detections offshore of the GOA, Mizroch and Rice (2013) found little evidence of seasonal site fidelity. For example, this suggested that the sperm whales' preferred habitat in August of one year, they may be over 1000 km away from their preferred location in August of another year. However, the whale distribution at historical whaling 'grounds' (certain areas with concentrated whaling effort) was consistent with preference for specific oceanographic features, coinciding with large scale frontal zones that concentrate nutrients and prey (Mizroch and Rice, 2013).

Commercial whaling extensively targeted and reduced the population of sperm whales in the Pacific Ocean. Between 1908 and 2009, a total catch of 316.902 sperm whales was reported in the entire Pacific, whereas from 1761 to 1920 the locations of 36.909 sperm whale kills by Yankee whalers was reported

(Mizroch and Rice, 2013). The sperm whale hunt persists even today, in Lamalera (Indonesia) where a small catch of sperm whales is allowed with the use of primitive methods, and in the Pacific by Japan that is allowed by the International Whaling Commission (IWC) to take 0–10 animals per year for 'scientific' purposes, since 2000 (Whitehead, 2018). Nowadays, conservation concerns related to the sperm whale populations in the Pacific are likely related mainly to effects from global warming and anthropogenic noise (Harris et al., 2015). Although the sperm whale is among the best-studied cetaceans, and the Alaska waters have been surveyed extensively, large gaps remain including temporal patterns (in interannual and seasonal scale) in inaccessible offshore areas of the GOA.

1.6 Objectives

The principal goal of this thesis is to enrich the understanding of the ecology of sperm whales in the open ocean. The overall objective is to use passive acoustics to identify key marine habitats important for sperm whales and examine their habitat preferences over a range of temporal scales and geographic locations.

1.7 Thesis Outline

Here, I present research into the temporal patterns of sperm whale acoustic occurrence in the Subarctic North Pacific and the Eastern Mediterranean Sea, with a particular focus on the environmental drivers of the observed patterns (for the Pacific data set), including assessments of the ambient sound levels of the soundscape that the whales occupy. An integral part of this dissertation, included in Chapters 2-4, focuses on the acoustic recorder's ability to detect sperm whales and assess temporal patterns, examining potential biases that may occur from using a non-continuous acoustic recorder.

Chapter 2 describes the analysis of passive acoustic recordings from the Greek Seas. It includes examination of temporal patterns of the sperm whale and delphinid detections in two sites of the Aegean and the Ionian Seas, and measurements of the noise levels and their seasonal variability at both locations.

Chapters 3 and *4* use a five-year-long acoustic data set with recordings from the offshore Gulf of Alaska to investigate the seasonal and interannual variability of the sperm whale acoustic presence at the Ocean Station PAPA. The major objective of this dissertation is to quantify sperm whale habitat preferences in the subarctic Pacific, explaining the temporal patterns observed, using a suite of oceanographic variables. The modeling efforts described in Chapter 4 attempt to investigate the relationship between sperm whale acoustic occurrence and large-scale climate fluctuations, El Niño events and ocean warming.

Each chapter in this dissertation is published. Thus, Chapters 2-4 are written as stand-alone papers, likely causing some repetition between Chapter 1 (general introduction) and the introductions of Chapters 2-4. Version of Chapter 2 is published in the *Mediterranean Marine Science* Journal, and Chapters 3 and 4 are published in the *Deep-Sea Research I* Journal.

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2. Year-round acoustic presence of sperm whales (*Physeter macrocephalus*) and baseline ambient ocean sound levels in the Greek Seas

An evening in the Aegean includes sorrow and joy in so equal doses
that nothing is left but the truth.

Ένα δειλινό στο Αιγαίο περιλαμβάνει τη χαρά και τη λύπη σε τόσο
ίσες δόσεις που δεν μένει στο τέλος παρά η αλήθεια.

— Odysseas Elytis, Μύρισαι το Αριστον (XIV)

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2.1 Abstract

The sperm whale (*Physeter macrocephalus*) is the largest odontocete occurring in the Greek Seas. However, monitoring the species' spatiotemporal distribution patterns is especially difficult during the winter months when unfavorable weather conditions often hinder survey efforts. In the Greek Seas, visual cetacean surveys are typically not conducted between November and March. In a first attempt to collect year-round baseline information on sperm whale occurrence patterns in Greek waters, two Passive Aquatic Listeners (PAL) were deployed for 19 months, at Pylos Station (36.8 N, 21.6° E) in the Hellenic Trench, and at Athos Station (40.0 N, 24.7° E) in the North Aegean Trough. Results revealed the year-round presence of sperm whales at Pylos Station with a higher number of detections observed during late spring and throughout the summer. No sperm whale vocalizations were detected at Athos Station. An ambient sound level analysis revealed higher winter and lower summer levels at both sites largely driven by local weather conditions. Results showed that marine life in the Hellenic Trench area was exposed to higher low frequency (< 1 kHz) sound levels (by up to 10 dB re 1 $\mu Pa^2/Hz$). Ambient noise below 1 kHz is frequently dominated by anthropogenic sources including shipping. Ship strikes and noise disturbance constitute major threats for the small, genetically isolated, endangered sperm whale population. The results of this study are useful for sperm whale conservation efforts in the region and may help policymakers in prioritizing mitigation measures, including the establishment of speed limits and rerouting of ship traffic.

2.2 Introduction

Sperm whales (*Physeter macrocephalus*) inhabiting the Greek Seas are part of the Mediterranean Sea population, which is genetically isolated from its adjacent Atlantic population (Engelhaupt *et al.*, 2009) and listed as 'Endangered' by the International Union for Conservation of Nature (Notarbartolo-di-Sciara *et al.,* 2012). The sperm whale population in the Greek Seas is very small and believed to consist of less than 250 individuals (Frantzis *et al.*, 2014a); about 12% of the entire Mediterranean Sea population (Rendell & Frantzis, 2016). The Hellenic Trench, located in the Ionian Sea (Figure 2.1), concentrates the majority of those 250 individuals and has been described as a sperm whale hot spot in eastern Mediterranean Sea (Boisseau *et al.*, 2010; Frantzis *et al.*, 2014a). Consequently, under the Agreement for the Conservation of Cetaceans of the Black and Mediterranean Seas, this area has been assigned as an *Important Marine Mammal Area* and is being considered as a designated *Marine Protected Area (MPA;* IUCN-MMPATF, 2017). Information on sperm whales in the Aegean Sea is sparse and largely limited to reports of opportunistic sightings for the North Aegean and the Ikarian Troughs (Frantzis, 2009).

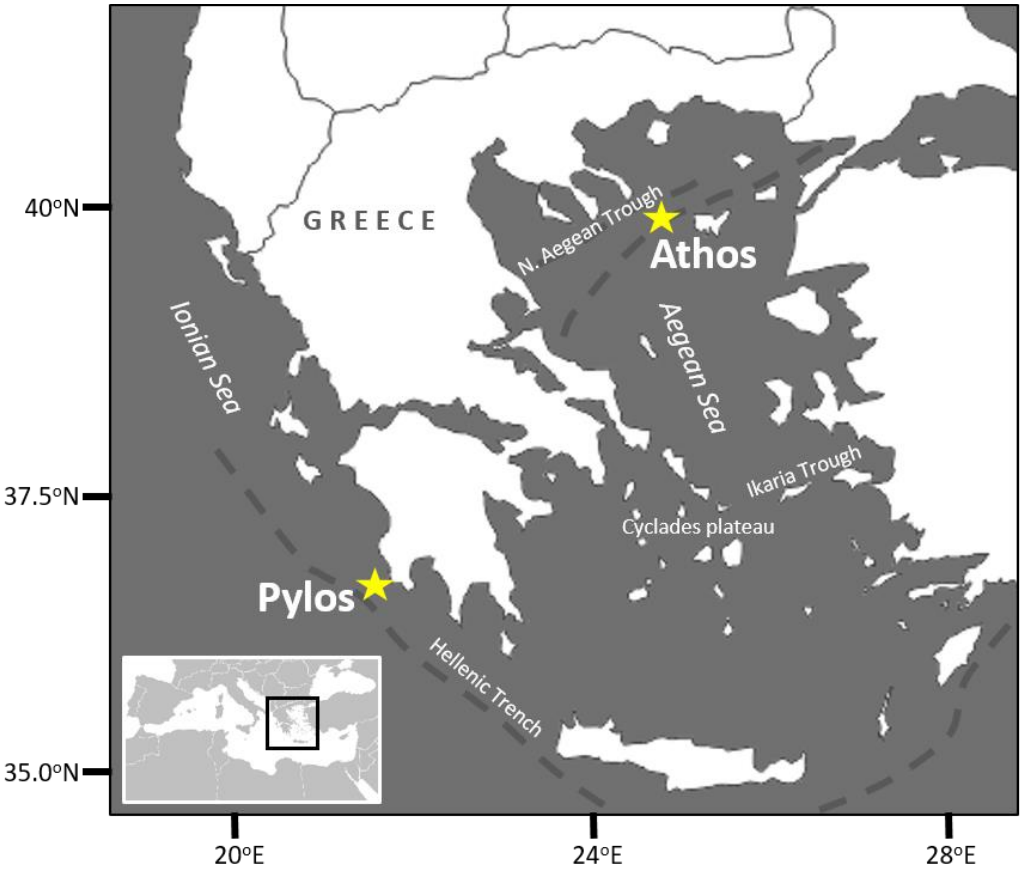

Figure 2.1 - Location of the POSEIDON buoys where the Passive Acoustic Listeners (PALs) were deployed and the acoustic sampling was implemented. The Hellenic Trench and the North Aegean Trough are shown in dashed lines in the main map and the position of the Greek Seas in the Mediterranean is shown in the bottom left frame.

In the Hellenic Trench, the sperm whale population consists of both mature males and social units of adult females with their young indicating that this area is an important nursing and breeding ground (Frantzis *et al.*, 2014a; Frantzis *et al.*, 1999; Rendell and Frantzis, 2016). Even though their only natural predator, the killer whale (*Orcinus orca*), is not abundant (Notarbartolo Di Sciara, 1987) and whaling never occurred within the Mediterranean Sea, other anthropogenic activities (e.g., ship strikes) threaten the sperm whale population in this area (Notarbartolo-Di-Sciara, 2014;

Rendell and Frantzis, 2016). In the Greek Seas, levels of marine traffic are especially high along the Hellenic Trench (Frantzis *et al.*, 2014a; Frantzis *et al.*, 2015). In addition to ship strikes (Frantzis *et al.*, 2015; Campana *et al.*, 2015), further concerns exists about potential negative impacts of increased vessel noise on the whales (Weilgart, 2007, Erbe *et al.,* 2015). The Greek government's recent plan for offshore oil and gas exploration in the Hellenic Trench area (YPEKA, 2018) constitutes another potential threat to sperm whales and marine life in general.

To establish effective conservation measures for sperm whales, year-round studies and knowledge on habitat use are essential (Levin *et al.*, 2014; Mannocci *et al.*, 2018). For many parts of the Greek Seas, information on sperm whale spatiotemporal distribution patterns are still lacking (Rendell and Frantzis, 2016). The Aegean Sea has been monitored the least for cetaceans among the Greek Seas (Mannocci *et al.*, 2018). Mannocci *et al.* (2018) also highlighted the need to relate patterns of cetacean presence to local levels of ship traffic and underwater noise.

Obtaining a long-term time series of cetacean presence using traditional visual surveys is a difficult task, especially for deep-diving, offshore species such as sperm whales. Due to the deep (up to 1800 m; Oliveira *et al.*, 2013) and long dives (up to 50 min; Aoki *et al.*, 2012) of sperm whales, it is difficult to detect them visually even in good weather conditions. The high costs associated with offshore research cruises also contribute to the lack of data in the eastern Mediterranean Sea. However, sperm whales are highly vocal animals which can be readily monitored using passive acoustic monitoring (PAM) techniques (Mellinger *et al.*, 2004). Sperm whale clicks (left panel, Figure 2.2) are broadband, impulsive signals which are about 30 ms in duration and highly directional featuring peak frequencies between 10 and 15 kHz (Møhl *et al.*, 2003). The clicks also feature a nearly omnidirectional low frequency (1-4 kHz) component (Zimmer *et al.*, 2005). This part of the click can be acoustically detected independently of the orientation of the animal towards the acoustic sensor. Sperm whales produce different patterns of clicks with distinct inter click intervals (ICIs). 'Usual clicks' with an ICI of 0.5-1.0 s are the most common signals and primarily used for prey detection. 'Creaks' with an ICI between 0.01-0.4 s are used to follow prey at close distances and are indicative of prey catching attempts (Wahlberg, 2002). 'Slow clicks' with an ICI of 5-8 s are mostly produced by males at breeding grounds and thought to be used for communication and advertisement. 'Codas' exhibit irregular ICI but stereotyped patterns of clicks that are repetitive and linked to communication and social interactions (Teloni *et al.*, 2008).

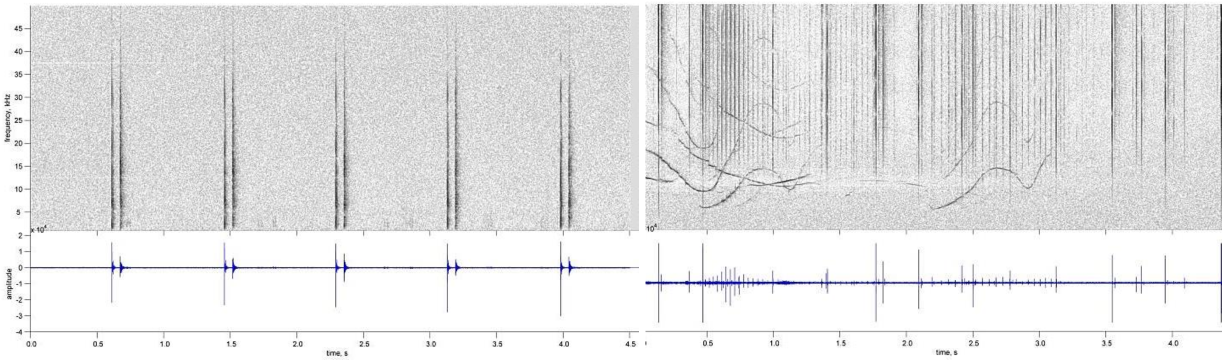

Figure 2.2 - Spectrogram (1024 Fast-Fourier Transform, Hamming window, 50% overlap) (top panels) and waveform (bottom panels) of sperm whale usual clicks (on the left; showing clicks and their echo) and delphinid clicks and whistles (on the right) recorded by a Passive Aquatic Listener (PAL) (duration: 4.5 sec, sampled at 100 kHz) at Pylos and Athos station, respectively.

Current monitoring efforts in the eastern Mediterranean Sea are largely based on visual surveys, which at times include the use of towed acoustic arrays (Frantzis *et al.*, 2014). However, to be able to monitor both cetaceans and ambient sound levels over extended periods (months to years) at locations of interest, the use of stationary autonomous recorders is a more effective method. Two autonomous acoustic recorders, Passive Aquatic Listeners (PALs), were deployed at Stations Pylos and Athos to investigate occurrence patterns of sperm whales and ocean sound levels in the Greek Seas between 2008 and 2010.

2.3 METHODS

2.3.1 Data collection and analysis

To assess sperm whale occurrence patterns, two Passive Aquatic Listeners (PALs) were deployed on oceanographic moorings as part of the POSEIDON II project (Nittis et al., 2002). The first PAL was deployed at Pylos Station (36.8 N, 21.6o E; 1680 m water depth) in the Ionian Sea. The second PAL was deployed at Athos Station (40.0 N, 24.7o E; 400 m water depth) in the North Aegean Sea (Figure 2.1). The PAL at Pylos Station (hereafter referred to as Pylos) was deployed at a depth of 500 m, approximately 10 km off the west Peloponnese coast and operated between 11 November 2008 and 8 July 2010. A 72-day gap in the acoustic data occurred from 19 September until 28 November 2009 due to a delay in the mooring maintenance cruise. The PAL at Athos Station (hereafter referred to as Athos) was deployed at 200 m depth approximately 30 km offshore between the Athos Peninsula and the island of

Limnos. The sampling period at Athos lasted 9 months, from 5 November 2008 to 8 July 2009.

The PAL, an autonomous passive acoustic recording system, collects data at a low duty cycle (1.5%) to achieve year-long deployment durations (Anagnostou *et al.*, 2011). For this study, the PAL was configured to wake up from sleep mode every 5 min to collect 4.5 s of acoustic data sampled at 100 kHz. The 4.5 s snippet (hereafter referred to as sound bite) was analyzed with an onboard energy detector for acoustic signals of interests and the sound bite was stored when a non-stationary (transient) acoustic signal, typically representing biological sound sources, was recognized. In order for the algorithm to detect a signal, the energy level in the 1-20 kHz band had to exceed a detection threshold of 12 dB compared to the average spectrum. The specific triggering frequency band was chosen to cover the omnidirectional part and peak frequency of the sperm whale clicks (1-4 kHz [Zimmer et al., 2005] and 10-15 kHz [Møhl et al., 2003], respectively). If a signal of interest was detected, the wakeup time was reduced from 5 min to 2 min until (a) no additional detection occurred, or (b) a daily quota of stored sound bites was reached (typically 6 per day). The decrease in sampling interval allowed more sound bites to be stored during the presence of signals of interest. If the quota at any given day was not reached, the following day's quota was increased by the number of remaining sound bites. Due to limitations in data storage capacity (~2 GB), the PAL's total per-deployment quota was 2200 sound bites, resulting in a total of 165 min of acoustic recordings during a one-year deployment. If no signal of interest was detected or the daily quota was reached, the PAL calculated and stored eight spectrum level curves (0.5-50 kHz) based on 10.24 ms of data separated by 0.6-0.7 s. While these spectrum levels could not be used to reliably detect sperm whale clicks, they provided valuable and continuous information on ambient sound levels in the sampling areas.

The PAL's subsampling strategy did not limit the detectability of sperm whale or other odontocete echolocation signals. Given that sperm whales vocalize continuously for 30-45 minutes during each dive with an average ICI of 0.6 s, a 4.5 s sound bite generally contains seven echolocation clicks. Under these conditions, the probability of detection is nearly 100%. However, the detectability of sperm whale clicks is limited with regards to the available daily quota of sound bites. This is of particular concern when other vocal species occur frequently at the deployment sites. When acoustic signals emitted by these species are present early in the day, the daily quota can be exhausted within the first hour of the day.

2.3.1.1 *Sperm whale detections*

The collected sound bites were converted to WAVE (.wav) audio files and manually screened by an experienced analyst (ND) for sperm whale and other marine mammal vocalizations. For this purpose, the Matlab-based program Osprey (Mellinger, 1995) was used to create spectrograms (Figure 2.2) using a Fast Fourier Transform size of 1024 points (Hamming window) with 50% overlap.

The data were used to report the daily presence or absence of sperm whale clicks, and high frequency delphinid clicks and whistles or pulsed calls (or 'burst-pulses') for each station. At least two clicks were required to confirm a sperm whale acoustic encounter. The manually annotated daily presence/absence of sperm whale and delphinid calls was binned by month and analyzed for temporal patterns. Each monthly time series was normalized by the number of sampling days within each bin. The data was used to assess seasonal and annual variability in the sperm whale and delphinid occurrence patterns.

Because of the PAL's sampling scheme, more common species in the deployment area typically took up most of the available sound bites and thus reducing the detection likelihood of lesser common species. Therefore, the relationship between sperm whale and other odontocete detections was investigated. All detections were grouped into three categories: (a) only sperm whale signals present in the sound bite, (b) only delphinid signals present in the sound bite, and (c) both sperm whale and delphinid signals present in the sound bite. In a second step, the occurrence of each category throughout the entire sampling effort was investigated.

In addition, the number of vocalizing sperm whales was estimated for each sound bite containing sperm whale vocalizations. Discriminating individual sperm whales involved manually grouping at least two similar usual clicks into single click trains. Clicks were grouped based on ICI, amplitude, and frequency characteristics (Figure 2.8; Appendix) (Ward, 2002). Vocalizing sperm whales were classified into three categories: (a) 1, (b) 2, and (C) 3+ animals.

2.3.1.2 *Operator error at Pylos, assessment of biases*

At Pylos, an operator error occurred when the unit was programmed, which resulted in a reduced sound bite duration of 2.5 s (instead of 4.5 s) for data recorded during the first 9 months of the deployment (November 2008 – July 2009). With an average ICI of about 0.7 s, at least two sperm whale usual clicks should have been recorded in the shorter sound bites still allowing for the identification and classification of the species. However, to evaluate the potential reduction in the analyst's ability to detect sperm whales in the shorter sound bites, a resampling experiment was conducted using 103 sound bites of 4.5 s duration containing sperm whale signal that were recorded in 2010. From each of these 103 sound bites, 2.5 s of continuous data were randomly extracted and re-analyzed. Results were compared to infer potential biases in detection performance.

2.3.1.3 *Modeling sperm whale detections*

Temporal patterns in sperm whale acoustic occurrence, and effects of both non-target species detections and the shorter duration sound bites, were evaluated using a generalized linear model (GLM) in R software (R Core Team, 2017). Logistic regression with a logit link function was used with the 'glm' function in the R package 'stats' to model sperm whale acoustic presence in each sound bite throughout the sampling period as a function of four predictor variables. The presence/absence of sperm whale clicks in each recording was used as the response variable (SW). To investigate seasonal patterns, month or season, defined as winter (December-February), spring (March-May), summer (June-August), and fall (September-November), were included as categorical explanatory variables in different models. In each GLM model, the presence/absence of delphinid signals (DELPH) was included as categorical explanatory variable. A binary dummy variable (SB) indicating the duration of the sound bite (0: 4.5 s, 1: 2.5 s) was included as a predictor to test potential effects of the reduced recording effort on the sperm whale detectability. The Akaike Information Criterion (AIC) was used for model selection.

2.3.2 Ambient sound levels

To assess baseline ambient sound levels for both study areas, calibrated spectrum levels stored by the PAL were analyzed. To assess the geographic variation in ambient sound levels, spectral probability density plots (SPD) were generated for both locations (Merchant *et al.* 2013). The PAL spectral data provided location-specific information on typical sound level distributions for the monitored frequency band (0.5 – 50 kHz). The 1st, 5th, 50th, 95th, 99th percentiles were computed for the available data sets. In addition, median daily values of ambient sound levels at 0.9 kHz and 3 kHz were compared between the two study areas and analyzed for seasonal patterns.

Median daily wind speed values from the POSEIDON buoys (http://env1.hcmr.gr/db_poseidon/) at Pylos and Athos were used to relate ambient sound levels to prevailing weather conditions. As the wind speed data from the Athos buoy were only available for the first 50 days of the deployment, additional data collected by the Hellenic National Meteorological Service (EMY; http://www.hnms.gr/emy) on Limnos Island (39.92° N, 25.24° E; closest anemometer to Athos) was included in the analysis. Cross-correlation function (CCF) plots of the wind speed and the 0.9 kHz and 3 kHz sound levels at each site were examined to assess the relationship between ambient sound levels and weather conditions. For Athos, a CCF plot of the wind-speed time series from the two data sources (POSSEIDON buoy and EMY) was examined to evaluate the similarity of the data sets.

2.3.3 Detection range

An important consideration when interpreting the results of PAM studies is the effective monitoring radius. The detection distance of a target signal depends on factors such as the source level, the ambient sound levels, bathymetry, the water column properties, and the detection threshold (Au and Hastings, 2008; Helble *et al.*, 2013). The average detection range of sperm whale clicks (specifically the low-frequency omnidirectional part) was modeled for both locations and investigated for temporal and spatial variability. For this purpose, the variation of sperm whale usual clicks' detection range between seasons at each location was assessed and compared among sites. Seasonal sound speed profiles for both station locations were downloaded from the World Ocean Database 2009 (WOD09, 2018). A BELLHOP model (Porter and Bucker, 1987) was applied to the data to estimate the propagation range of the omni-directional, low-frequency part of the sperm whale usual clicks. Detection distances were modeled for sperm whales vocalizing at 300 m and 900 m depth at Pylos, and 300 m depth at Athos. The usual clicks' source level was assumed to be 155 dB re 1 µPa^2/Hz at 3 kHz (Zimmer et al., 2005). The required ambient sound levels at 3 kHz for each season and location were extracted from the spectrum level data collected by each PAL (see section 2.2.). The PAL's detection threshold of 12 dB was added to the ambient sound levels to estimate the detection distance.

2.4 Results

2.4.1 Acoustic detections

In total, 4711 sound bites (4114 from Pylos and 597 from Athos) were collected during the 503-day observation period between 5 November 2008 and 8 July 2010.

2.4.1.1 *Pylos Station*

Sperm whales were present at Pylos during all months of the year that recording took place. No data was collected in the month of October, so sperm whale presence or absence cannot be confirmed (Figure 2.3). Sound bites were recorded during 479 out of 497 deployment days. Out of the 4114 total sound bites recorded at Pylos, 235 contained sperm whale vocalizations (5.7%). Sperm whale acoustic signals were recorded on 62 days (13%) and 17 out of the 19 months with observations (Figure 2.3). Most sperm whale detections were of usual clicks, but creaks and codas were also detected. It was not possible to verify the occurrence of slow clicks because the ICI associated with this signal type exceeded the duration of the recorded sound bites. Two types of codas were recorded: the ‘progressive’ or ‘expanding’ coda type (Weir *et al.*, 2007; Frantzis and Alexiadou, 2008) were detected in September 2009, and the typical ‘3+1’ type (Pavan *et al.*, 2000; Frantzis and Alexiadou, 2008) in March, April, and May 2010. The sperm whale detections did not show any obvious seasonal pattern over the course of the study (Figure 2.3). However, slightly increased detection rates occurred during the spring and early summer months (March until July) in both 2009 and 2010. No sperm whales were detected in December 2009 and July 2010, but their presence was confirmed in December 2008 and July 2009.

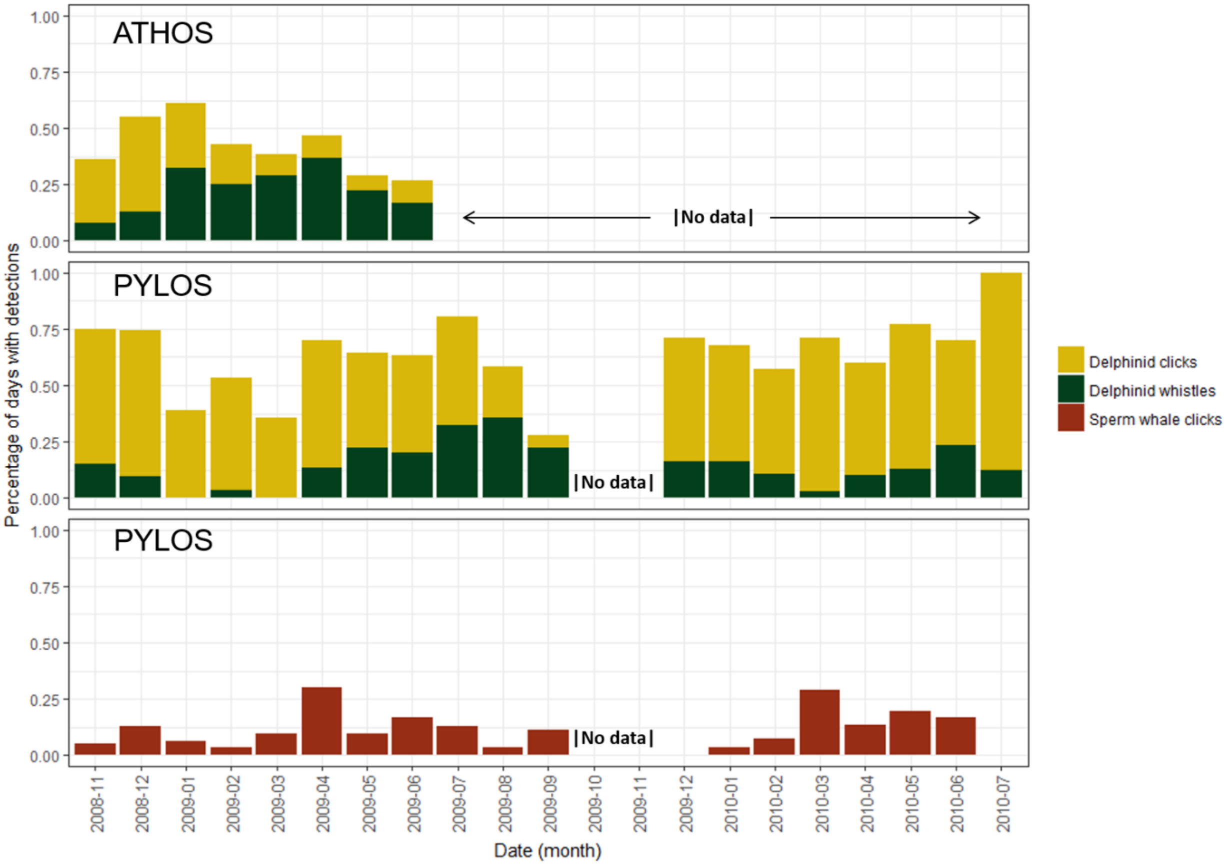

Figure 2.3 - The normalized monthly sperm whale and delphinid (clicks and whistles) acoustic detections at both Athos (panel on the top) and Pylos Station (middle and bottom panels), in the Eastern Ionian and the North Aegean Seas. Sperm whale detections were only detected at Pylos. The percentage of days with sperm whale detections per month are shown for the sampling period, November 2008 - July 2010. The highest number of days with sperm whale detections at Pylos was recorded in April 2008 (0.3).

The delphinid detections included click trains, burst-pulse calls and whistles. At Pylos, delphinid vocalizations were detected consistently throughout the sampling period during 390 of 479 days (81.4%). Whistles were detected during only 78 out of 479 days with recordings (16.3%) (Figure 2.9; Appendix). Out of the 4114 total sound bites recorded at Pylos, 2123 contained delphinid vocalizations (51.6%) and most of the remaining recordings contained anthropogenic noise attributed largely to nearby vessels. Of the 2123 sound bites with delphinid detections, 1995 contained exclusively clicks (94 %) and 128 contained whistles with and without clicks (6%). Delphinid calls did not show a consistent seasonal pattern, but the number of detections dropped by almost 40% from January to March 2009. The lowest detection rates were noted for September 2009. Detection rates remained consistently high throughout 2010 (Figure 2.3).

In many cases, sperm whale clicks and delphinid signals were detected within the same sound bites (Figure 2.10; Appendix). Specifically, of the 235 sperm whale detections, 45% contained both sperm whale and delphinid signals (55% contained exclusively sperm whale vocalizations). The recordings were also analyzed for sperm whale group sizes. Results indicated that groups of at least three sperm whales were detected in March, April, June, July, and September 2009, and from February through June 2010; while individuals and groups of two animals were detected during all months of the year (Figure 2.4). Most detections with more than one individual occurred during the spring and summer months, while fall and winter exhibited mostly detections of individuals (Figure 2.4).

Figure 2.4 - The number and proportions of recordings in a day (counting all sound bites) with each class of sperm whale counts ('1', '2', and '3+') in a weekly (top figure) and monthly (bottom figure) scale respectively for the entire duration of the sampling effort. Note that only the months that included sperm whale detections are shown. Since November 2008 until end of September 2009, the sound bites used were of half duration because of an operational error.

2.4.1.2 *Athos Station*

Between November 2008 and July 2009, 597 sound bites were recorded at Athos. Detections occurred on 139 days out of 192 sampling days. Even though many odontocete acoustic signals (not classified to species level) were recorded throughout the deployment period, no sperm whale acoustic presence could be confirmed. Delphinid clicks, burst pulse calls, and whistles were identified in 373 sound bites (63% of the recorded sound bites). Exclusively delphinid clicks were recorded in 266 sound bites (71% of the sound bites containing delphinid signals) while pulsed calls with and without clicks were detected in 107 sound bites (29%). The remaining sound bites contained anthropogenic noise, most frequently cavitation noise emitted by nearby vessels. The click detections corresponded to 108 days of delphinid presence (78% of the sampling days), and the whistle detections (often recorded with clicks) were noted on 58 days (41.7%). Because of the shorter observation period, information on seasonality of delphinid occurrence patterns at Athos is limited. However, results indicated that for the observation period, the number of detections was increased during the winter months December and January. (Figure 2.3, top panel).

2.4.1.3 *Investigations of detection biases due to shorter sound bites*

The data set that included the 2.5-s sound bites had also an issue with electronic noise, which resulted in frequent false positive detections that reduced the number of useful sound bites by approximately 50%. Only 46% of the stored sound bites contained sperm whale or delphinid signals. The analysis of the resampled sound bites from the 2010 data set showed that in 81 instances (79%) the sperm whale presence could still be identified in the shorter duration sound bites. However, the results clearly indicated that the reduced duration of the sound bites resulted in an underestimation of sperm whale detections. Because of the additional electronic noise issue, the available data could not be corrected for potential missed detections.

2.4.1.4 *Modeling sperm whale detections*

The model that included the months of the year had the lowest AIC score and was selected over the model with the seasons. However, both models revealed a significant negative impact on sperm whale detectability in the 2.5-s sound bites. Additionally, both models indicated a significant negative relationship between the detectability of sperm whales and the detection of any delphinid acoustic signal. Overall, the model with month, SB, and DELPH as predictor variables had the lowest AIC, and was selected as the best model. The best model was used to predict the temporal variability of the probability of sperm whale detections conditional on the absence of delphinid acoustic signals in the sound bites and the use of 4.5-s long sound bites. The model predicted the lowest detection probability for August and January and the highest detection probability for September (Figure 2.5). Higher probability was also predicted for March, April and June (Figure 2.5). No data were available for the month of October for any of the sampling years.

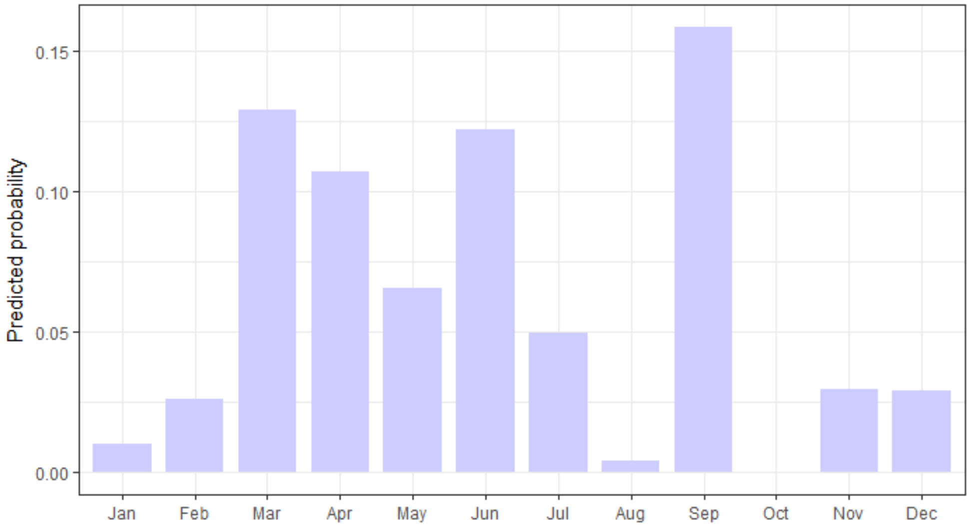

Figure 2.5 - The variability per month of the predicted probability to detect sperm whale clicks in a single sound bite at Pylos Station. These values represent the GLM model predicted results where we accounted for the effect of month, and conditioned for the absence of detections of delphinid sounds and the use of full 4.5-s sound bites.

2.4.2 Ambient sound levels

The ocean ambient sound level analysis provided a high-level picture of the variability in ambient sound levels in the Ionian Sea and the North Aegean Sea throughout the deployment duration. In addition, these data were used to assess the detection range of sperm whales at Pylos and Athos. The empirical probability density plots (Figure 2.6) indicated that the median (50th percentile) spectrum levels at the 0.9 kHz (indicative of shipping activity) were about 64 and 59 dB (re 1 $\mu Pa^2 Hz^{-1}$ throughout unless otherwise mentioned) at Pylos and Athos, respectively (grey dashed lines in Figure 2.66). The SPD plots also showed that the mean ambient sound levels at the low frequency where sperm whales clicks are omnidirectional (3 kHz, grey solid arrows in Figure 2.6) were 55 dB at Pylos and 50 dB at Athos. It should be noted that the SPD levels for Pylos and Athos should not be directly compared because the data sets encompass different deployment durations.

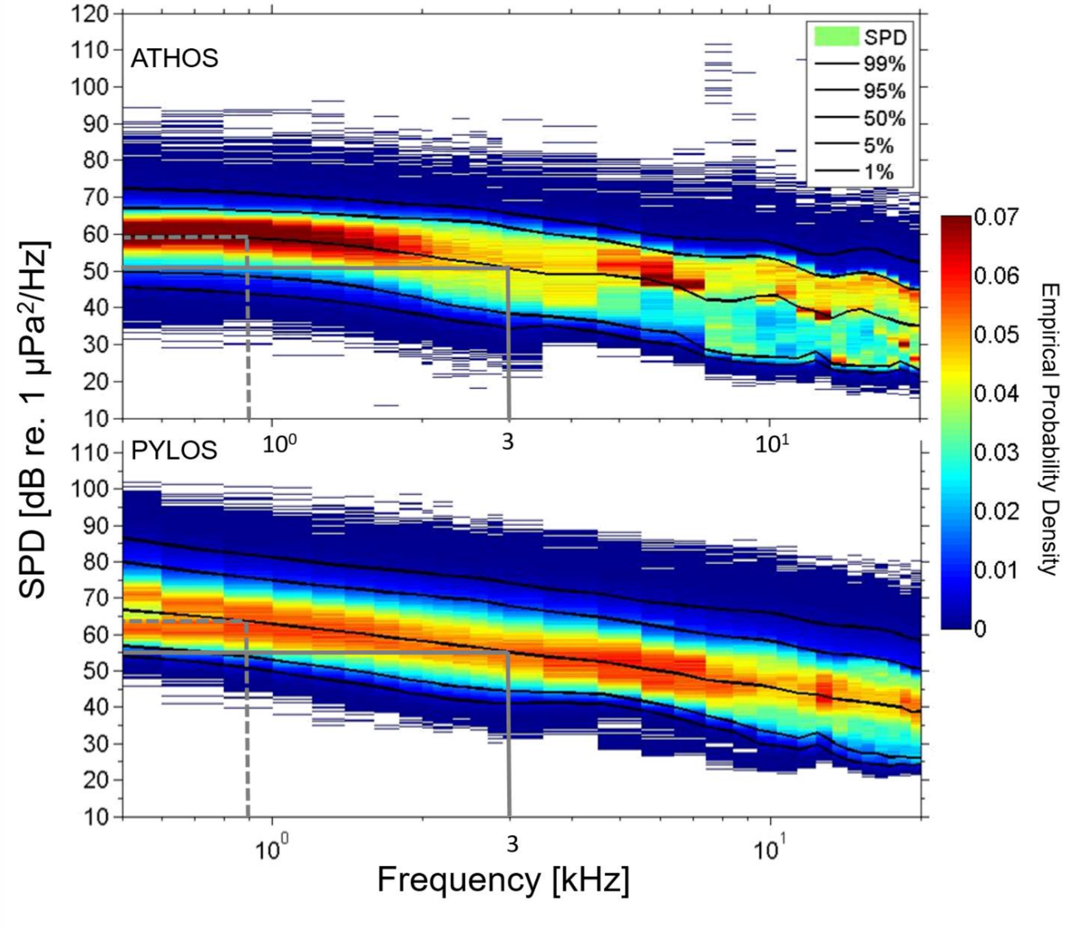

Figure 2.6 - Spectral probability density (SPD) plots for the stations of Athos (top) and Pylos (bottom) calculated by the almost continuous records of individual spectral data. The colors indicate the likelihood of a given spectral level in a specific frequency band. The 1%, 5%, 50%, 95%, 99% percentiles are shown in this order with black contour lines from the bottom upwards. The solid grey arrows connect the median (50th percentile) sound level to the frequency where sperm whale vocalizations are omnidirectional (~3 kHz). The dashed grey lines connect the median sound level to

the frequency at 0.9 kHz, below which ambient sound levels are indicative of shipping activity

Seasonal variability of daily sound levels was significant at both sites (Figure 2.7). At Pylos, median (50th percentile) levels at 0.9 and 3 kHz were 4 dB and 5.5 dB higher in the winter compared to summer (0.9 kHz: 53 dB [1%], 76.5 dB [99%]; 3 kHz: 43.6 dB [1%], 69.2 dB [99%]). At Athos, median levels were about 7 dB (0.9 kHz) and 9 dB (3 kHz) higher during the winter months (0.9 kHz: 49.6 dB [1%], 69.4 dB [99%]; 3 kHz: 40.2 dB [1%], 62.8 dB [99%]). The median daily ambient sound levels at Pylos were 2-3 dB higher on average compared to Athos.

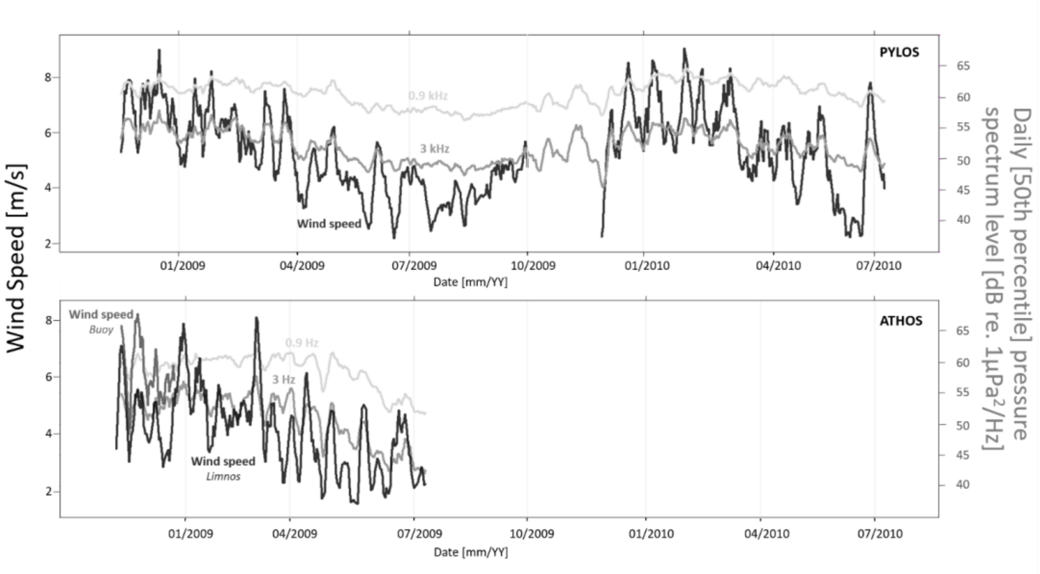

Figure 2.7 - Seasonal patterns of the daily median (50th percentile) 0.9 and 3 KHz spectrum levels and the wind speed in Pylos and Athos. All lines are smoothed with a 7-day moving average.

The observed seasonal patterns in sound levels at both frequencies (0.9 kHz and 3 kHz) were primarily related to non-biological sources. The CCF plots revealed a 68% and 85% correlation (zero lag) between the daily time series of the median wind speeds and the Pylos ambient sound levels at 0.9 kHz and 3 kHz, respectively. For Athos, the wind speeds measured at Limnos meteorological station showed a 57% and 75% correlation with the ambient sound levels at 0.9 kHz and 3 kHz (zero lag), respectively. CCF plots using wind speeds measured at the Athos buoy showed 88% and 93% correlation with the ambient sound levels at 0.9 kHz and 3 kHz (zero lag), respectively. Additionally, there was a high correlation between the wind speed values measured by the Limnos anemometer and the Athos buoy (86%, zero lag) indicating that the Limnos data is representative of the wind conditions at Athos.

2.4.3 Detection range

BELLHOP models were used to estimate the detection range of sperm whale usual clicks (low-frequency omnidirectional part). Results indicated seasonal detection radii of 13-22 km from the PAL deployed at Pylos, and 15-22 km from the PAL deployed at Athos (Table 2.1). Results indicate changes in the maximum detection ranges between seasons and for different depths of the simulated vocalizing whale (Table 2.1). At Pylos, the farthest detection ranges were modeled for summer (22 km) while no variability was observed between winter, spring and fall (13 km and 15 km for the 900 m and 300 m dives, respectively). The lowest median ocean ambient sound levels at 3 kHz were also measured in summer at Pylos (55 dB). At Athos, smaller detection ranges were observed for winter (15 km) and farther ranges for spring (22 km). These results corresponded to the seasonal highest and lowest median ambient sound levels measured at 3 kHz (54 dB and 44 dB). No data was available from Athos to assess the variability of ambient sound and detection ranges during summer and fall. A comparison between the two sites showed that similar ambient sound levels resulted the same detection ranges (Table 2.1).

Table 2.1. The variability of sperm whale click propagation range at Pylos and Athos Stations for different seasons. We used a simulation of usual clicks (with 155 dB re 1 μPa^2/Hz source level at 3 kHz) emitted at 300 m and 900 m depth for Pylos, and 300 m for Athos. In Athos, complete ambient sound data were available only for the winter and spring seasons.

	Propagation range [km] (Ocean ambient sound levels [dB re 1μPa^2/Hz])		
	ATHOS	**PYLOS**	
Whale depth	*300 m*	*300 m*	*900 m*
Winter	15 (66.2)	15 (67)	13 (67)
Spring	22 (61.5)	15 (64.4)	13 (64.4)
Summer	-	22 (61.4)	13 (61.4)
Fall	-	15 (63.5)	13 (63.5)

2.5 Discussion

2.5.1 Sperm whale presence

Autonomous passive acoustic recorders were deployed at two locations in the eastern Mediterranean Sea for which only limited data on marine mammal occurrence patterns exist (Mannocci *et al.*, 2018). Data analysis was challenging because of the duration and, at times, quality of the acoustic recordings. Nevertheless, the results provided valuable information on temporal occurrence patterns of cetaceans in the Greek Seas between November 2008 and July 2010. The results revealed that sperm whales were present during all seasons at Pylos, including the winter months and in most cases, more than one individual was detected in the recorded sound bites.

For the Hellenic Trench, the model results suggested a higher probability for sperm whale detections during late spring to early fall and a lower probability for the winter months. Throughout the winter months, a high number of delphinid detections was registered. The PAL's mode of operation likely contributed to lower sperm whale detections during this period. The model indicated the highest probability for a sperm whale detection to occur for the month of September. This was also the month with the lowest number of delphinid detections. In addition, September contained a high percentage of detections with sperm whale groups of three or more individuals (Figure 2.4), which may have increased the detection probability for sperm whales during this period. For these reasons, the reported sperm whale patterns are biased by the presence of delphinids and possibly by seasonal changes in sperm whale group sizes. Overall, the number of sperm whale detections reported for Pylos likely significantly underestimated the actual number of days that sperm whales were present at this location.

The absence of sperm whale detection from Athos was also largely unsurprising. Only a few sperm whale sightings and strandings have previously been reported for other parts of the Aegean plateau (Frantzis *et al.*, 2003), including the Chalkidiki Peninsula and Athos area (Frantzis, 2009). More recent PAM studies in the area failed to detect sperm whales (Ryan *et* *al.*, 2014). A plausible explanation for the absence of sperm whales at Athos is the shallow water depth (400 m). Sperm whales show clear preference for deeper habitats with steep bathymetric gradients (shelf breaks, seamounts, and canyons; Pirotta *et al.*, 2011; Frantzis *et al.*, 2014). The most frequent acoustic detections at Athos were associated with the presence of Risso's dolphin (*Grampus griseus*), which tends to inhabit the upper part of the continental slope habitat (Praca and Gannier, 2008).

2.5.2 Sperm whale detection range and ambient sound levels

A comparison of the two sites showed that the detection ranges of sperm whale usual clicks were the same between Athos and Pylos. Thus, the lack of sperm whale detections at Athos could not be attributed to unfavorable sound propagation conditions. At both sites, the largest variability in propagation distances (15-22 km) occurred between seasons and was driven by differences in ambient sound levels. Additionally, results from Pylos indicated that clicks emitted at 300 m during all seasons propagated farther than clicks produced at 900 m. Overall, during summer, depth of the vocalizing animal had the largest impact on detection distance (difference of 9 km; Table 2.1). During winter, spring and fall, the depth of the vocalizing animals had a minor impact on detection range (difference = 2 km). These differences are a result of the seasonal variability in the sound speed. The seasonal variability in ambient sound levels measured at Pylos and the corresponding variability in detection ranges likely contributed to biased sperm whale occurrence patterns (e.g. increased detection range during the summer would allow for a higher number of sperm whales to be detected). Overall, the detection range predictions agree with previous results from the Mediterranean Sea (André *et al.*, 2011).

At both sites, the seasonal variability of ambient sound levels at 3 kHz was strongly correlated with wind speeds. This relationship was weaker at frequencies below 1 kHz, indicating that other sound sources, such as shipping, contributed to the sound levels at these frequencies. In fact, during the summer, ambient sound levels at the shipping-relevant frequency (0.9 kHz) were up to 10 dB higher at Pylos compared to Athos. This was not surprising since shipping activities of large vessels are lower at Athos. Additionally, shipping activity in the Greek Seas typically intensifies during the summer months. Pylos, in particular, is located in the vicinity of a major shipping lane and marine animals in the Hellenic Trench are exposed to higher ambient sound levels.

The sperm whale population and their habitat in the Greek Seas are in need of targeted conservation efforts. No management actions for the protection of the species have been implemented by the Greek government. This study confirms the high importance of the Hellenic Trench for this small population. The proposed oil and gas exploration activities in that region, including seismic surveys and potentially drilling, could impair vital sperm whale life functions related to foraging, breeding, and nursing. In addition, the busy shipping lanes increase the risks of ship strikes. Passive acoustic monitoring is an efficient tool to cost-effectively study vocal cetacean species and anthropogenic noise levels for extended periods. The large data gaps reported for the eastern Mediterranean Sea (Mannocci *et al.*, 2018) can effectively be bridged with increased use of passive acoustics. In addition, acoustics is species-agnostic and can be used to monitor a wide variety of marine animals (cetaceans, fish, and crustaceans) simultaneously. An important research goal should be the establishment of long-term acoustic stations in the Greek Seas to monitor for shifts in ambient sound levels and cetacean occurrence patterns. This work also demonstrates that the PAL in its current configuration lacks the ability to document most fine-scale temporal occurrence patterns of cetacean species. With limitations in battery and memory capacity, the PAL allows long-term recordings of odontocete signals (high frequency sounds that require large memory) that are collected under a subsampling strategy rather than a continuous sampling scheme. The PAL's daily quota of acoustic files makes the assessment of temporal patterns in sperm whale occurrence challenging when other vocal cetacean species occur frequently at the deployment site. However, the collected data provides valuable information on year-round sperm whale presence and variability of the ambient sound levels at both sites. For marine mammal research, it would likely be better to increase the number of sound bites that PAL can store, and to not rely on the onboard detection algorithm. Instead, the PAL could store sound bites at a pre-defined interval throughout the deployment.

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2.7 Appendix

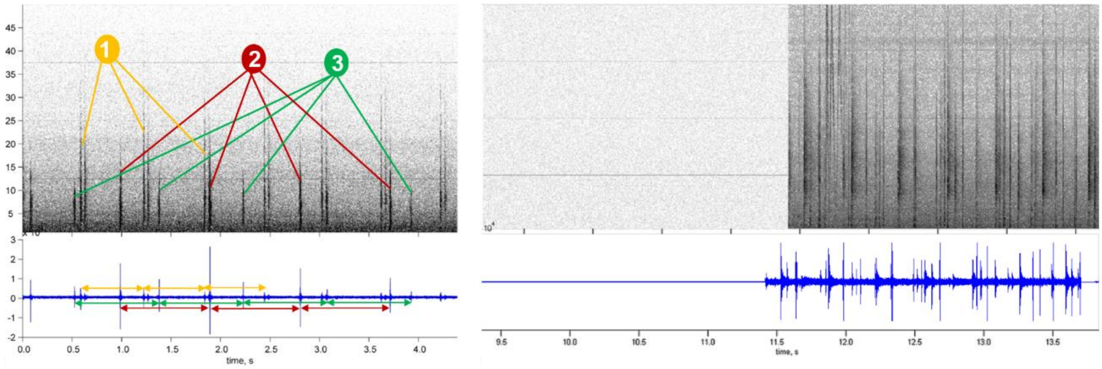

Figure 2.8 - Spectrograms (1024 Fast-Fourier Transform, Hamming window, 50% overlap) (top panels) and waveform (bottom panels) of sperm whale usual clicks from 3 individuals (the echo is shown for the first individual, on the left) and more than 3 animals (on the right) recorded by a Passive Aquatic Listener (PAL) (duration: 4.5 sec, sampled at 100 kHz) at Pylos station. With the same color arrows at the waveforms, the consistent inter click intervals (ICIs) and the gradual decay or increase in amplitude within clicks of the same click trains are indicated. The same color lines at the spectrograms and the waveforms indicate the clicks within one click train that have similar frequency range and belong to an individual whale. Note that the recording on the right represents a half-duration sound bite.

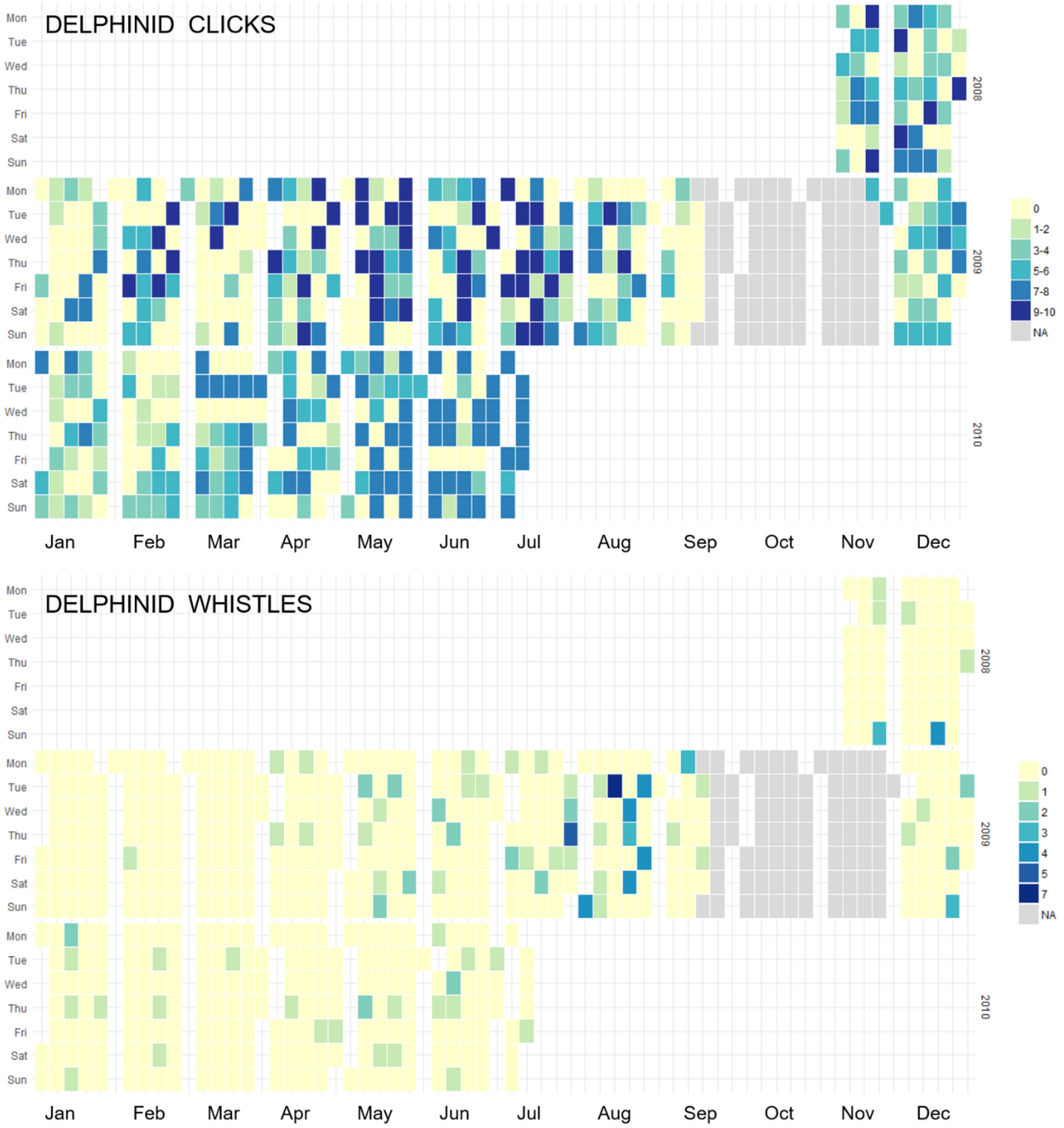

Figure 2.9 - Days with delphinid click detections (panel on top) and delphinid whistle detection (panel on bottom) at the recordings from Pylos Station over the sampling period, November 11 2008 until July 8 2010. A data gap, due to scheduled service interval of the oceanographic buoy, is shaded in grey.

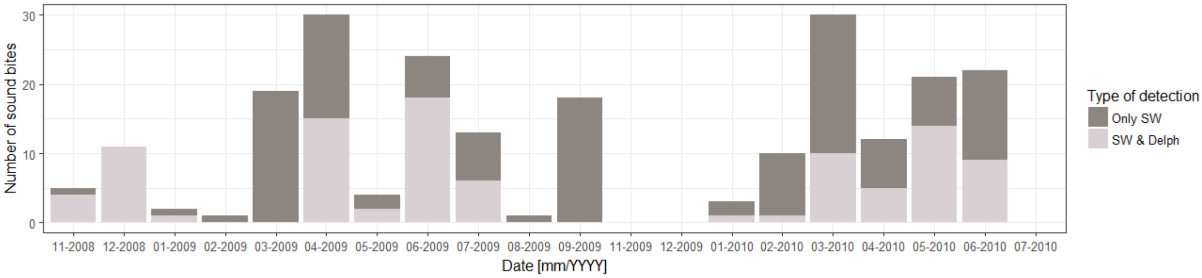

Figure 2.10 - The monthly variability of sound bite numbers that included sperm whale clicks at Pylos Station, grouped into two categories based on their coexistence with other odontocete acoustic signals. Each color represents a detection category: (a) only sperm whale clicks (dark grey), (b) sperm whale clicks and delphinid signals (light grey).

3. Sperm whale (*Physeter macrocephalus)* acoustic ecology at Ocean Station PAPA (Gulf of Alaska) – Part 1: detectability and seasonality

One doesn't discover new lands without consenting to lose sight, for a very long time, of the shore.

— André Gide, Les faux-monnayeurs

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3.1 Abstract

Sperm whales *Physeter macrocephalus* produce loud, stereotypical click sequences and are an ideal species to be studied with passive acoustic techniques. To increase our limited knowledge on sperm whale occurrence patterns in remote and inaccessible locations of the North Pacific, we analyzed a five-year-long (June 2007 – April 2012) acoustic data set recorded at Ocean Station PAPA (OSP; 50°N, 145°W) in the Gulf of Alaska (GOA). Firstly, we assessed the sperm whale detection performance of the Passive Aquatic Listener (PAL), and secondly, we investigated temporal patterns of sperm whale presence at OSP. The PAL proved highly efficient, with above 50% probability of detecting more than two sperm whales, a condition met for over 50% of the recordings. Results indicated that sperm whale clicks were recorded year-round, with a clear seasonal pattern. The number of detections during the summer months was approximately 70% higher compared to the winter. An ambient noise analysis showed that differences in detection rates were likely not driven by seasonal changes in ambient noise levels. The average propagation range of sperm whale clicks ranged between 7 and 8 km between summer and winter, with slightly decreased detection distances observed in winter. Seasonal shifts in the intensity of the Alaska Current and the latitudinal oscillations of the North Pacific Transition Zone results in changes in water mixing, transport of nutrients and the concentration of prey such as squid, which likely drives sperm whale distribution.

3.2 Introduction

The largest toothed whale, the sperm whale (Physeter macrocephalus), is globally classified as 'Vulnerable' under the criteria of the International Union for the Conservation of Nature. In the United States (US), environmental laws protect marine mammals from harassment, hunting, capturing, or killing, and aim to conserve endangered species and their habitats. The sperm whale is listed as 'Endangered' under the US Endangered Species Act and 'Depleted' under the US Marine Mammal Protection Act (NMFS 2013). These listings require the US government to establish and implement recovery plans for this species. One of the major challenges associated with the management and protection of sperm whales globally, and particularly in offshore locations, is the lack of reliable data on regional stock structure and population status (Perry et al., 1999). This information is crucial for the development of effective protection measures. Commercial whaling between the 18th and 20th centuries had a large impact on sperm whale populations, reducing their abundance by 68% worldwide (Whitehead, 2003). Although the species received full protection through an international moratorium on commercial whaling in 1985, current threats, with potential adverse population level effects, still exist and include the impact of climate change on habitat and prey, increasing underwater anthropogenic noise, collisions with vessels, interactions with fisheries, and chemical pollution (Whitehead, 2003). In the Gulf of Alaska (GOA), a designated Temporary Maritime Activities Area (Fig. 1) extends from the shelf region into deep offshore waters and is where the US Navy conducts training exercises. Naval activities, including the use of tactical mid-frequency active sonar and explosives, may pose a risk for cetaceans, particularly deep-diving species like sperm whales (Talpalar and Grossman, 2005).

Sperm whales spend most of their lives below the ocean surface (Irvine et al., 2017), which makes it difficult to observe them visually. Sperm whale foraging dives can exceed 1860 m and last for more than one hour (Teloni et al., 2008). Sperm whales are exceptionally vocal and use sound for foraging and communication. Their frequent vocalizations (85-91% of the dive duration; Mathias et al. 2012; Teloni et al. 2008) make this species an ideal candidate for passive acoustic monitoring (Mellinger et al., 2004). They produce sequences of loud clicks (223 dB re 1 μPa @ 1m; Møhl et al. 2000) that allow for passive acoustic detection over long distances (9-90 km; Barlow and Taylor, 2005; Madsen et al., 2002; Mathias et al., 2013) . Their acoustic signals typically include different patterns of clicks with a variable inter-click-interval (ICI). ICIs include: 5-7 s ICIs for 'slow clicks', produced mostly by males; 0.5-1 s for 'usual clicks', used for echolocation during deep dives; 0.02 s for 'creaks', believed to indicate prey capture attempts; and irregular ICIs for 'codas', linked to communication and socialization (Teloni et al., 2008). The duration of a usual click is about 30 ms (Møhl et al., 2003), and a sperm whale calling bout, associated with the vocally active part of each dive, lasts on average 30 min (Mathias et al., 2012; Teloni, Mark, Patrick, & Peter, 2008).

In the central and eastern North Pacific Ocean, population abundance estimates exist for sperm whales in the California Current (2539 animals; Moore & Barlow 2014), as well as for the Hawaiian Islands (4559 animals; Bradford et al. 2017). Density estimates (individuals per 1000 km^2) in the North Pacific were highest in the eastern temperate Pacific (3.4-4.2; Barlow and Taylor, 2005), lower in Hawaii (2.82; Barlow, 2006) and the US West Coast (1.7; Barlow and Forney, 2007), and overall higher compared to the global average (1.4; Whitehead, 2002). In the GOA, abundance estimates for sperm whales are limited, especially for the winter months, impeding appropriate management schemes for the species. Visual line-transect surveys conducted during the summer months of 1980 and 1994 (Forney & Brownell

1997, Rice & Wolman 1982) concluded that the population size in the offshore waters of the GOA and the eastern Aleutian Islands was small. Mellinger et al. (2004) collected three years of acoustic data to characterize sperm whale presence in the GOA and detected sperm whale clicks throughout the year, with higher presence during summer compared to winter. Additional data are required to more completely characterize the patterns of temporal occurrence of this species in the GOA.

In the subarctic North Pacific, Ocean Station PAPA (hereafter referred to as OSP) is a deep-ocean observation station in the GOA, part of the 'Line P' survey line (a network of 26 vessel sampling locations between the Strait of Juan de Fuca and OSP) (Figure 3.1). Consistent records of a variety of oceanographic variables have been collected along Line P and at OSP for over 60 years (Freeland, 2007) and numerous scientific studies focusing on lower trophic levels have been conducted (Boyd and Harrison, 1999; Peña and Varela, 2007; Whitney and Freeland, 1999). To-date only one study focused on apex predators (Dall's porpoises *Phocoenoides* dalli, Pacific white sided dolphins *Lagenorhynchus obliquidens*, and a variety of pinnipeds and marine birds) along Line P. The eight-year study's primary goal was to assess habitat preferences for the species of interest. Visual observations were collected during spring and summer surveys; OSP was not included in the study as rough weather conditions significantly hindered survey efforts and resulted in an insufficient number of observations (Yen et al., 2005).

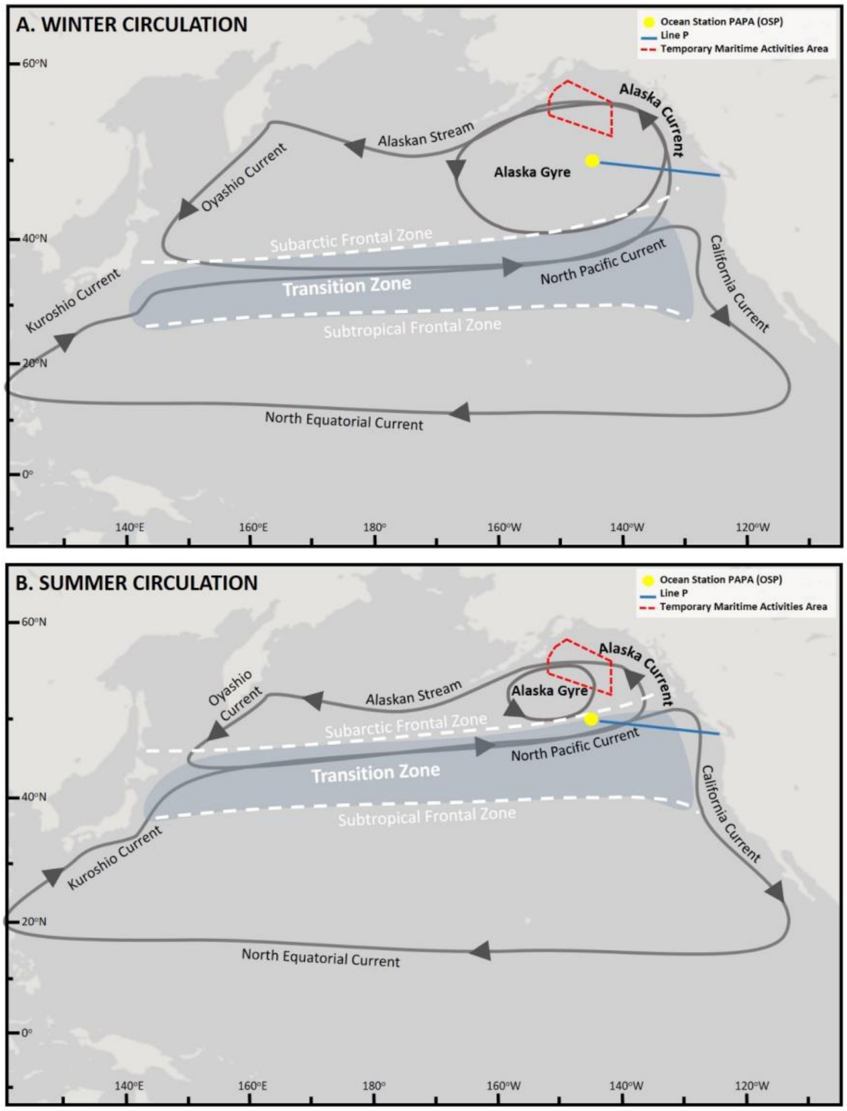

Figure 3.1 - Location of the Ocean Station PAPA (OSP) buoy (yellow circle) where the Passive Aquatic Listener (PAL) was deployed and the acoustic sampling was conducted. Also indicated: the Line P survey line (blue line), along which a long-term oceanographic time series has been collected; the location of the U.S. Navy's Temporary Maritime Activities Area (red box); and the major circulation pattern during the winter (A) and summer (B) months in the North Pacific and particularly the Gulf of Alaska (GOA). (Maps are adapted and redrawn from: Pearcy, 1991; Pacific North

Coast Integrated Management Area Initiative, 2011; Tomczak & Godfrey, 2001; Whitney et al., 2005; Block et al. 2011).

Acoustic methods are an efficient tool to detect vocalizing cetaceans such as sperm whales (Whitehead and Gordon 1986, Barlow and Taylor 2005). Underwater acoustic recording technologies have improved over the last few decades (Mellinger and Bradbury 2007) allowing collection of data on cetacean presence in a non-invasive and cost-effective manner, especially in remote locations (Mellinger et al., 2002). Fixed recorders provide long time series of cetacean acoustic detections that are needed to detect changes in distribution patterns (Silber et al., 2017). In order to extract and evaluate the information contained in long-term recordings, robust detection and classification of acoustic signals is required. To achieve this, data are visually inspected or automatic detection algorithms are applied. Passive Aquatic Listeners (PALs) were originally designed and used to monitor precipitation and wind speed at sea through the quantification of ambient sound (Anagnostou et al., 2011; Nystuen, 1998). PALs have previously been used to detect sounds from fin whales (*Balaenoptera physalus*), humpback whales (*Megaptera novaeangliae*), North Pacific right whales (*Eubalaena japonica*), gray whales (*Eschrichtius robustus*), killer whales (*Orcinus orca*), bowhead whales (*Balaena mysticetus*), and a variety of pinniped species (Denes et al., 2014; Hanson et al., 2013; Miksis-Olds et al., 2007), and to assess these species temporal occurrence in the Bering Sea and the continental shelf of the US West Coast (Hanson et al., 2013; Miksis-Olds et al., 2010). However, sperm whales are not common in those shallow-water areas and, for that reason, were not included in these studies. Another study from the Eastern Mediterranean Sea used PALs to detect sperm whale presence (Diogou et al., 2019).

In this study, we evaluated the ability of the PAL to detect and record sperm whale clicks in order to investigate the seasonal presence of sperm whales in offshore GOA waters. Specific steps included (1) assessing the variation in the probability of detecting sperm whales with the PAL subsampling strategy, (2) evaluating potential ambient noise masking effects on sperm whale detection efficiency, (3) investigating the seasonal variability in propagation range of sperm whale calls, and (4) identifying and quantifying potential temporal occurrence patterns in the data.

3.3 Materials and Methods

3.3.1 Study area

The study area was the GOA, in the subarctic North Pacific, in the vicinity of the OSP located 913 km away from the nearest shore. Seafloor topography at OSP is characterized by a few scattered seamounts (Figure 3.1), while the oceanography is defined by its location at the southern edge of the Alaska Gyre (Harrison et al., 1999). Ecologically, the subarctic Pacific is a temperate ecoregion and one of the world's major 'high-nitrate, low-chlorophyll' regions, characterized by consistently low phytoplankton and chlorophyll-*a* (Boyd and Harrison, 1999; Boyd et al., 1995). Nitrate rarely becomes depleted in these waters (Peña and Varela, 2007), while iron and low sunlight during the winter moderate phytoplankton growth and productivity (Boyd et al., 1996; Maldonado and Price, 1999). The coastal GOA is a highly productive ecosystem with upwelling taking place in the summer and sustaining rich fisheries. In contrast, at OSP, an increase in levels of chlorophyll-*a* is consistently associated with eddy transport of coastal iron offshore (Whitney and Robert, 2002)that in turn results in a high diversity of marine mammals, seabirds, plankton and fish. Cetaceans encountered in the offshore GOA range from small-sized odontocetes such as the Dall's porpoise *(Phocoenoides dalli)* to large mysticetes such as the blue whale (*Balaenoptera musculus*), fin, humpback, right, killer, and sperm whales, (Mellinger et al., 2004; Rone et al., 2017; Stafford et al., 2007). A variety of seabirds found there include black-footed albatross (*Pheobastria nigripes*), tufted puffin (*Fratercula cirrhata*), fork-tailed and Leach's storm-petrel (*Oceanodroma furcate, Oceanodroma leuchora*), and dark sheawaters (*Puffinus spp*.). Dominant zooplankton found at OSP include euphausiids and pteropods with mean lengths of 15 and 1.5 mm, and myctophid fishes of 28 mm length, with the latter showing an increase in abundance in May (Trevorrow, 2005).

3.3.2 Data Collection and Analysis

3.3.2.1 *Instrumentation*

To assess sperm whale occurrence patterns, we deployed a PAL (Anagnostou et al., 2011; Nystuen, 1998) at OSP (A'Hearn et al., 2013; OCS, https://www.pmel.noaa.gov/ocs/moorings) at 50°N, 145°W and a depth of 190 m (water depth approximately 4200 m). Data were collected over a five-year period, from 6 June 2007 to 15 April 2012. The PAL is a battery operated, high-frequency autonomous recorder of sea state zero noise level (Anagnostou et al., 2011). The frequency bandwidth of the recordings (0.5-50 kHz) covered the entire frequency range of sperm whale vocalizations (0.2-32 kHz) (Madsen et al. 2002).

The PAL's sampling strategy involved waking up from a 'sleep' mode every 5 min throughout the day to collect 4.5-s-long acoustic samples (hereafter referred to as sound bites) at 100 kHz sampling rate. An onboard real-time event detector evaluated each sound bite in order to identify the presence of non-stationary acoustic signals, typically occurring from biological sound sources. The energy detector, used for a preliminary evaluation of the sound sources, involved calculating and comparing eight spectrum level curves (0.5-50 kHz) based on 10.24 ms of data separated by 0.6 and 0.7 s. This way, eight sub-sampling detection cycles occurred within each sound bite. A sound bite was stored when at least one of the eight curves deviated from the average and spectrum levels exceeded a detection threshold of 12 dB within the predefined frequency band (2-25 kHz; targeting sperm whales but also included other odontocete species) for this study. If a stationary signal (typically associated with geophysical sounds such as wind and rain) was detected, the sound bite was discarded, the average spectrum of the eight curves was stored, and the next sample was taken in 5 min. Alternatively, the detection of a signal of interest (non-stationary) triggered a decrease in the sampling interval to 2 min until (a) the signal of interest was not detected, or (b) a daily quota of sound bites was reached. The PAL's memory capacity (~2 GB) limited storage of sound bites that contained targeted signals to six sound bites per day (quota), or about 2200 bites (165 min of acoustic recordings) during the each deployment. On days that the quota was not reached due to the absence of biological sound sources, the unused sound bites were available to be recorded on the following days, resulting in up to 22 sound bites to be stored per day.

This flexible sampling strategy resulted in a variable duty cycle: on days when there are no clicks detected, the PAL sampled every 5 min for 4.5s, saved none of the sound bites, and the duty cycle for the day was 1.5% (100 x 1296/86400 = 1.5%); on days when clicks occurred continuously, the quota would fill early in the day, and the apparent daily duty cycle could decrease to 0.03% (100 x

27 / 24 x 60 x 60 = 0.03 %). This seemingly low vigilance time would not, however, adversely affect our results because we simply tallied presence or absence of clicks per day, independent of when they occurred or how many times they occurred in each day. The sound bites could not be used to investigate diel click patterns but we feel confident that they were a reliable indicator of daily sperm whale presence, while the average spectra data provided valuable information on ambient sound levels for the area.

3.3.2.2 *Sperm whale detections*

Sperm whale vocalizations (Figure 3.2) are broadband, impulsive clicks with peak frequencies between 10 and 15 kHz. A nearly omnidirectional low frequency component (1-4 kHz; Zimmer *et al.*, 2005) allows sperm whale clicks to be acoustically detected independently of the whale orientation towards the hydrophone. Acoustic data sets (consisting of a series of 4.5-s sound bites) were converted to WAVE (.wav) files and were visually and aurally analyzed by an expert (ND) for sperm whale vocalizations. With OSP located more than 900 km offshore, absence of interferences from intense shipping noise or delphinid vocalizations facilitated the discrimination and accurate classification of the sperm whale clicks. Spectrograms (Figure 3.2) were generated and inspected in the Matlab-based program Osprey (Mellinger, 1995) using a Fast-Fourier Transform size of 1024 with 50% overlap (5.5 ms time resolution) and a Hamming window. Presence or absence of sperm whale clicks (and other cetacean vocalizations) was noted for every sound bite (that were stored for containing signals of interest) and daily presence was recorded. Sperm whale click patterns were inspected in detail to classify the different sperm whale click types based on their ICI. The sampling period was divided into 5-day bins that each included the sum of days with sperm whale detections, taking values from zero to five. When a 5-day bin fell between two months (i.e. 2 days in November and 3 days in December), it was attributed to the month with more days in the bin (i.e. December). The resulting time series was used to investigate patterns in sperm whale occurrence in the study area.

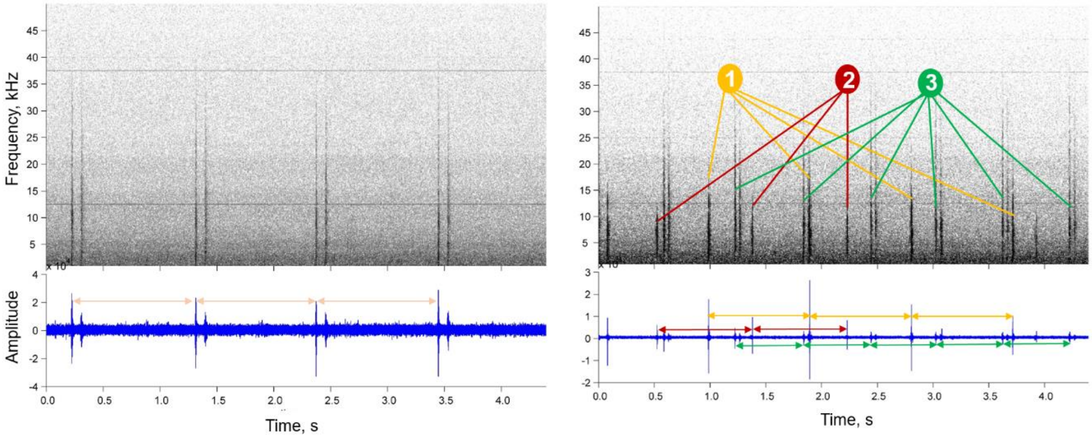

Figure 3.2 - Spectrogram (top panels) and waveform (bottom panels) of sperm whale acoustic signatures recorded by the Passive Aquatic Listener (PAL) (duration: 4.5 s, sampled at 100 kHz) at Ocean Station PAPA (OSP). Shown are the usual clicks by one (left plot), and three individuals (right plot). Individual click trains, distinguished by the waveforms, the consistent inter click intervals (ICIs), similar frequency range, and the gradual decay or increase in amplitude, are color-coded.

3.3.2.3 *Evaluation of PAL's detector performance for sperm whales*

The probability of detecting a sperm whale that occurs in the vicinity of the PAL depends on two factors: the calling behavior of the whale and the detection performance of the recorder (Fais et al., 2016). We estimated the probability of detecting sperm whales by examining the timing of the subsamples occurring relative to the whale's clicking. Following a brute force computational approach, we calculated the probability (P_n) that at least one sperm click will be detected within the PAL's eight detection cycles. This detection probability was based on when the first click would occur within the 4.5-s sound bite, which determined whether this click or any of the rest of clicks from the same click train (one individual) would be detected. Finally, P_n was estimated as:

$$P_n = \frac{D}{T} \qquad [1]$$

where D is the sum of the possible instances that a click could overlap with one of the eight subsamples of a sound bite. T is the duration of each ICI examined.

Running through all possible patterns of click occurrences within a sound bite, D was estimated based on the number of subsamples (a), subsample duration (b), effective click duration (c), and ICI. A formula was designed which provided a matrix of all possible click detections based on simulations of click occurrences with 1 ms resolution over the entire sound bite.

For the probability calculations, the detection subsamples were considered relative to their location within the click events and the specific ICIs. Additionally, each of the eight subsamples was treated as if it happened in an instant, which was defined as the end point of the subsampling detection window. Directionality of the clicks was not included in the calculation of the detection probability, because usual clicks have a low-frequency component (between 1 and 3 kHz) that is omnidirectional and can help with detectability (Zimmer et al., 2005). The duration of each subsampling cycle within the sound bites was 0.6 and 0.7 s and the spacing of the subsamples was at 0.0, 0.6, 1.2, 1.9, 2.5, 3.1, and 4.4 s.

ICI can vary considerably depending on the type of vocalization. For this calculation, the ICI of usual clicks was used, which can range between 0.2-2 s, and most frequently varies between 0.6 and 0.8 s. This click type is produced during 75-85% of dives at high latitudes (Mathias et al., 2012; Teloni et al., 2008; this study). We used 0.7 s as an average value, but calculated all probabilities for ICIs of 0.2 to 2 s every 1 ms, and used the average probability for 100 ms centered at each ICI (0.2, 0.3, 0.4 etc.). Slow clicks and codas occur more frequently at lower latitudes and breeding grounds (Madsen et al., 2002; Weilgart and Whitehead, 1988), and with the creaks that follow long sequences of usual clicks were excluded from these calculations. Additionally, the long ICI of the slow clicks (5-7 sec) would not allow for their detection in the 4.5 sec sound bites. Therefore, only usual clicks were analyzed.

Equation [1] was also used to calculate P_n for different numbers of vocalizing sperm whales (P) defined as:

$$P = 1 - (1 - P_n)^i \qquad [2]$$

where i was the number of whales.

Then, we assessed the variability of whale counts throughout the year. Hand processing of clicks and manual counts of whales from acoustic recordings is a time-consuming and tedious task. Thus, we used a subset of the 2010-2012 data that includes the strongest anomalies of sperm whale detections, and manually counted all sperm whale echolocation clicks recorded in each sound bite. Discrimination at the individual whale level was done by grouping clicks in a click train based on their similarity (Figure 3.2). Indications of click similarity included measuring and visually identifying, both in spectrograms and waveforms, three key features: (a) consistent ICIs, (b) similar frequency range, and (c) similar amplitudes of clicks of the same click trains. ICI patterns alone have been found to be an effective means of differentiating between individual sperm whales (Ward, 2002). At least three clicks with the above features were required to characterize one click train and classify one individual whale. We grouped all counts into three classes: (a) 1-2, (b) 3-4, and (c) 5+ whales. These classes corresponded to certain probabilities of detection calculated from Eq. (1-2) for the different numbers of whales present. Then, in order to evaluate the variability of numbers of whales in a day, we calculated the proportion of sound bites within each class in a day's recordings. Further, these daily proportions were aggregated in a monthly scale over all years to evaluate the variability of sperm whale group sizes throughout the year. Sound bites that included other sounds that could trigger the PAL detector, such as high-frequency clicks and whistles from other odontocete species, were removed from the analysis. The purpose of counting sperm whales was to provide an estimation of the variation in the probability of a sperm whale appearing in the recordings and not to estimate population density.

3.3.2.4 *Ambient noise levels*

Ocean ambient noise can mask acoustic signals and significantly reduce the area over which a vocalizing whale can be detected (Helble et al., 2013). To examine the effect of background noise on the detection range of sperm whale signals at OSP, we assessed the baseline noise levels for the region using the calibrated power spectra saved by the PAL. Specifically, real-time processing of the PAL's time series included eight 10.24 ms subsamples spaced 0.6 and 0.7 s apart. Each of the subsamples was run through a Fast-Fourier Transform to obtain a 512-point (0-50 kHz) power spectrum. The power spectra were then spectrally compressed to 64 frequency bins, with a frequency resolution of 200 Hz from 100 to 3000 Hz, and 1 kHz from 3 to 50 kHz. The average spectrum was stored internally every five minutes throughout the duration of the deployment, providing an almost continuous record of ambient sound levels.

Spectral probability density plots (SPD) were used to assess ambient noise levels and their temporal variation (Merchant et al. 2013). SPD used both conventional percentiles and spectral averages. We applied SPD on the PAL spectral data in months with the minimum and maximum sperm whale detections to provide an indication of sound level distribution in each frequency band. The 1st, 5th, 50th, 95th, 99th percentiles and the root-mean-square (RMS) were computed for each power spectrum. Values of median noise in the 3 kHz band (the omnidirectional low-frequency band of sperm whale clicks) were compared between periods in a year with minimum and maximum sperm whale occurrence.

3.3.2.5 *Propagation range*

We also investigated the seasonal variation of the propagation range of sperm whale clicks to ensure that the temporal patterns in sperm whale occurrence were not an artifact of seasonal changes in propagation conditions. The seasonal averages of the sound speed for the water column down to the seafloor (4235 m) were calculated from temperature and salinity measurements extracted from the Generalized Digital Environmental Model (GDEM, Version 2.5) provided by the U.S. Navy (Allen, 2012) for the summer and winter. The sound speed profile information was imported as the Sound Velocity Profile and used in a BELLHOP algorithm to assess the sound propagation in the area (Porter and Bucker, 1987). To predict the acoustic ray path arrival angles and received levels, we used a hypothetical sperm whale vocalizing at different depths (50, 100, 250, 500, 750, 1000, and 1500 m). The ambient sound levels used were extracted from the calculations of this study (see section 2.2.4) in the sperm whale vocalization omnidirectional low frequency of 3 kHz. The PAL's detection threshold of 12 dB was added to the ambient sound levels to estimate the detection distance. Propagation range calculations were made for clicks of +/- 90 degrees beam angle. The sperm whale click source level used was 155 dB re 1 $\mu Pa^2/Hz$ for a single frequency of 3 kHz (Zimmer et al., 2005), much lower (as expected) than the 223 dB that refer to the broadband level. The average detection range was calculated for all modeled depths and for each season.

3.3.2.6 *Seasonality*

Analysis of seasonal trends was done using the sperm whale acoustic occurrence patterns at OSP over five years. To statistically quantify observed seasonality, we applied a locally weighted regression fit (loess) (Cleveland et al. 1992) in the R language for statistical computing (R Core Team, 2017) based on the day of the year centered on each 5-day bin of the sperm whale detection time series (with values between 1 and 365; following Zuur et al. 2009). The window width m (or the size of window span, S) of the loess smoother was chosen (loess.as function in the fANCOVA R package)(Wang, 2012). For the selection of the optimal span value, the Akaike information criterion (AICC) method was used. To examine the goodness of fit of the loess model we used the diagnostic tools available in the R package 'car' (Fox et al., 2011). Model residuals were evaluated for heterogeneity and over-dispersion as well as for autocorrelation using plots of residuals against time, and autocorrelation function (ACF) plots (Ramsey and Schafer, 2002). A Kruskal–Wallis test was performed on monthly averages of sperm whale detections. The 'kruskal.test' function (R package 'stats') was used to compare the sperm whale occurrence among seasons (fall: September-November, winter: December-February, spring: March-May, summer: June-August) using the percentage of days with sperm whale detections per month as the unit of analysis. A post hoc pairwise Wilcoxon rank sum test ('pairwise.wilcox.test' function in the R package 'stats') identified significant differences between seasons.

3.4 RESULTS

3.4.1 Acoustic detections

Sperm whales were detected acoustically in all months throughout the five-year sampling period (except for a six-month data gap in 2010 due to delayed maintenance of the mooring). Out of the 7268 total sound bites recorded during the 1605 survey days, sperm whale vocalizations were observed in 6114 sound bites (84%) during 1142 of the days (71%) (Appendix, Figure 3.2). Usual clicks and creaks, but no codas, were identified throughout the sampling period. The temporal occurrence of sperm whale detections over the course of the study is illustrated in Figure 3.3.

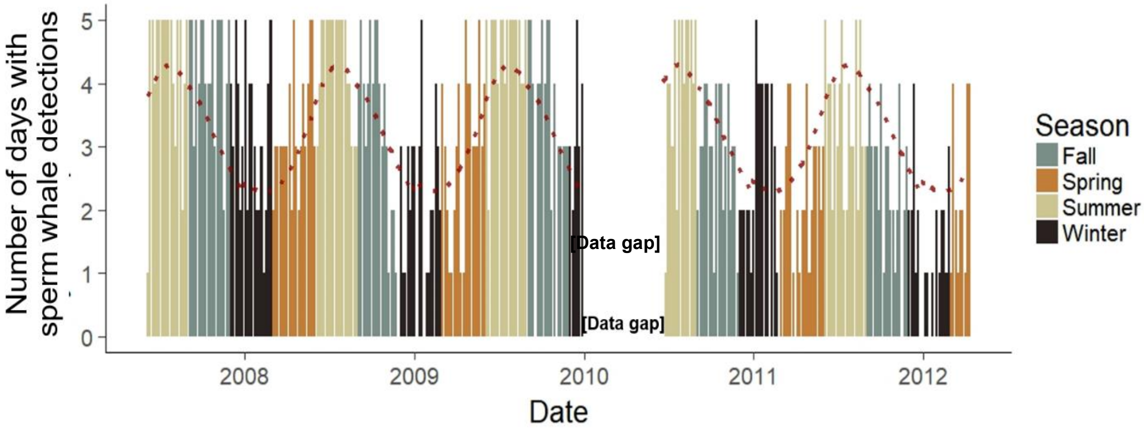

Figure 3.3 - Time series of sperm whale acoustic detections at Ocean Station PAPA (OSP), emphasizing the seasonal pattern. The amount of days with sperm whale detections within 5-day bins are shown for the sampling period June 2007 - April 2012. Each bar represents a 5-day bin and the different colors indicate the seasons (fall [blue]: September-November, winter [black]: December-February, spring [orange]: March-May, summer [khaki]: June-August). The dotted red line represents the seasonality of sperm whale occurrences at OSP modelled as a smooth function of the day of the year using locally weighted polynomial regression (loess).

3.4.2 Evaluation of PAL's detector performance for sperm whales

Assuming 10 ms effective click duration and 0.2-2 s ICI, we estimated 2-11 sperm whale clicks to occur in a 4.5-s sound bite. Thus, the probability of detecting one vocalizing sperm whale with the PAL’s onboard detector during at least one of the eight subsamples was between 8-57% for usual clicks with a 0.2 to 2 s ICI and a 0.6-0.7 s sampling interval. At shorter ICIs, there was a higher probability for sperm whales to be detected by the PAL (Figure 3.4A). Specifically, at ICIs of 0.7 and 0.4 s, the detection probability was estimated to be 21% and 34%, respectively. However, a slight decrease in the detection probability occurred for ICIs that were in resonance with the sampling cycle (with a large greatest common denominator with 0.6; Figure 3.4A). In addition, at higher number of whales, the detection probability also increased. For two vocalizing sperm whales with 0.7 ICI, the probability to be detected by the PAL's onboard detector increased to 38%. For more than two individuals clicking at 0.7 ICI, the probability of detection was above 51%, reaching 70% and above when five and more animals were present (Figure 3.4B).

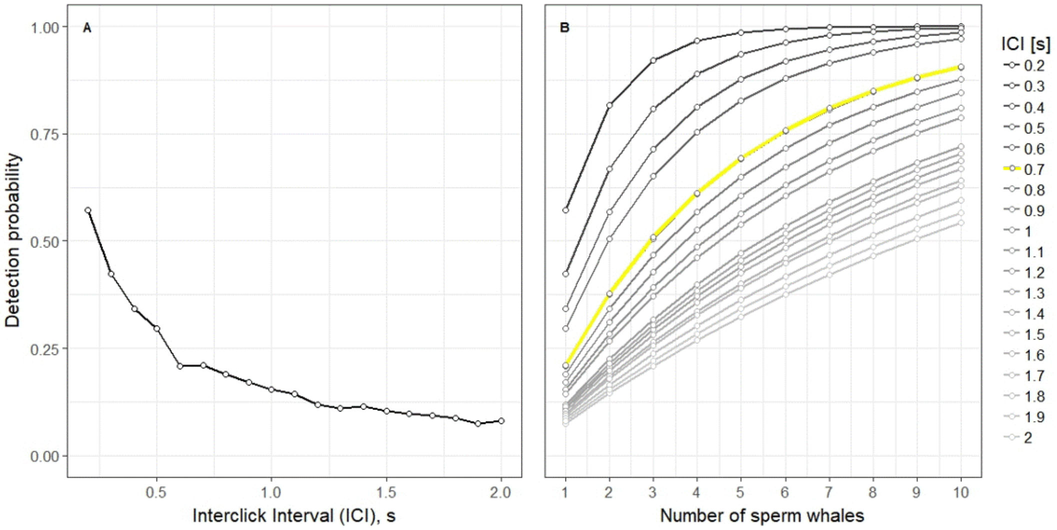

Figure 3.4 - The probability of detecting a sperm whale during a sound bite and its variability as a function of (A) inter click interval (ICI) for usual clicks, and (B) number of whales. The probability of detection is based on the 0.6-0.7 s subsampling interval of the detector of the Passive Aquatic Listener (PAL) and is given by Eq. (1-2). The probability for 0.7 s ICI and different number of whales is shown in yellow.

During the 2010-2012 recordings were analyzed for counts of animals; between one and five sperm whales were identified per sound bite. At times, more than five animals were clicking simultaneously; we were unable to accurately determine the number of individuals due to overlapping clicks, and thus the counts we report represent the minimum number of animals recorded by the PAL during the 4.5-s sound bite. Ninety-eight percent of the sound bites recorded during this period (2010-2012) included sperm whales clicks. Over 50% of the recordings with sperm whales obtained throughout the year included three or more animals (Figure 3.5), when the probability of detection was over 50% (Figure 3.4B). There was not a seasonal pattern in the proportions of daily recordings with three or four animals, maintaining a detection probability above 50% year round (Figure 3.5). However, larger groups (5+) appeared less common from December until February compared to other months (Figure 3.5). In addition, the days in which sound bites included only 1-2 whales were evenly distributed throughout the 2010-2012 data and did not indicate any obvious seasonal pattern.

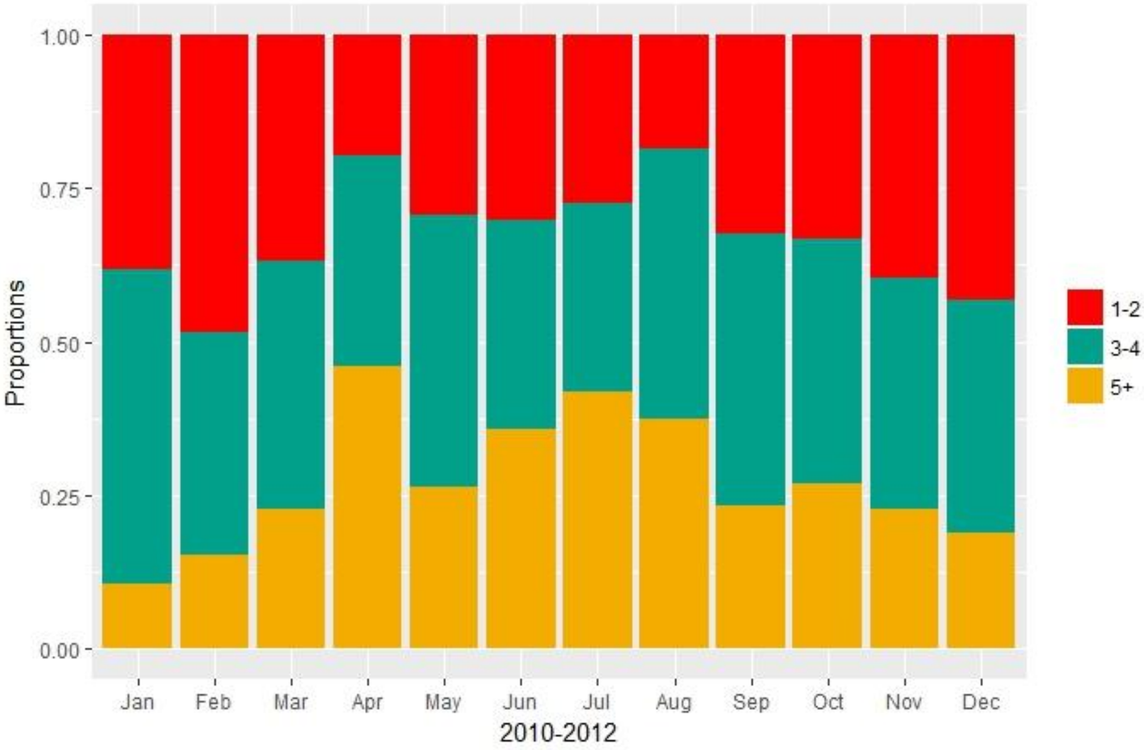

Figure 3.5 - The proportions of recordings in a day with each class of whale counts ('1-2', '3-4', and '5+') in a monthly scale and standardized. The '3-4' and '5+' classes together, representing a detection probability above 50%, are higher than 50% during all months and show no particular seasonality. A subset of the data (July 2010 to April 2012) was used for the analysis of whale counts.

3.4.3 Ambient noise levels

The SPD plots (Figure 3.6**Error! Reference source not found.**A and **Error! Reference source not found.**B) allowed us to investigate the potential ambient noise effect on the detectability of sperm whale signals between summer and winter of 2009 (Figure 3.6). We focused on this year specifically because the data set indicated the overall highest (July 2009) and lowest (January 2009) monthly sperm whale detections within one year (Figure 3.10). During both months (July and January), the median (50th percentile) ambient noise levels ranged between 53 and about 57 dB re 1 μPa^2/Hz in the 3 kHz frequency, where sperm whale clicks are omnidirectional.

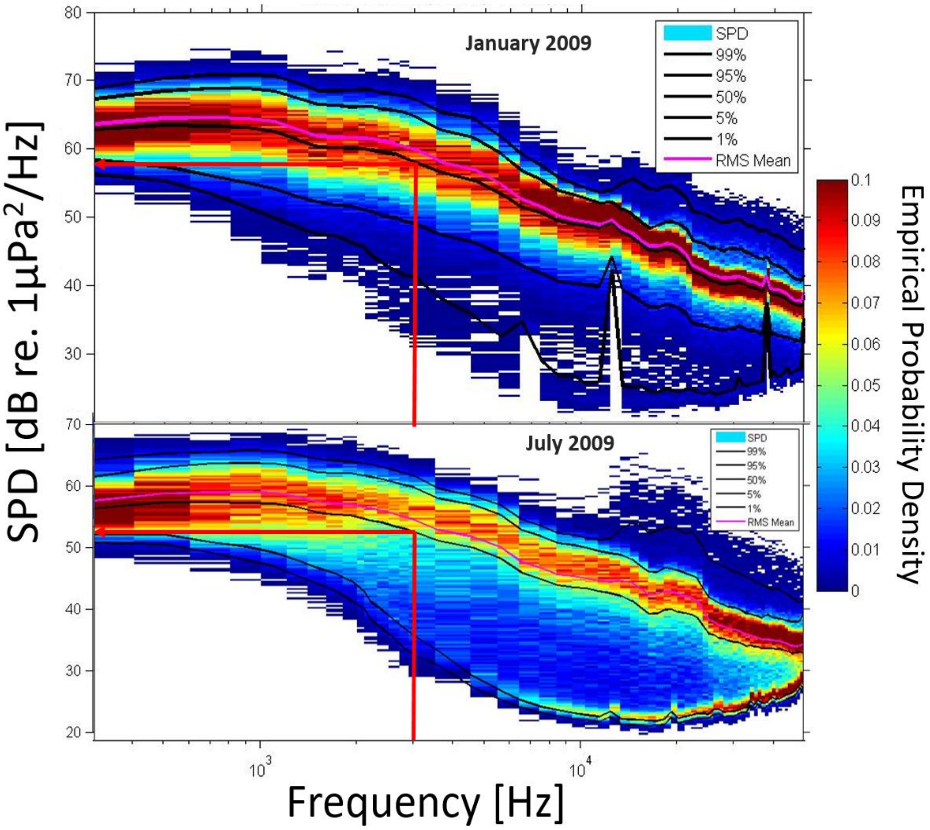

Figure 3.6 - Spectral probability density (SPD) plots for the months of January 2009 (top panel) and July 2009 (bottom panel) at Ocean Station PAPA (OSP) calculated by the almost continuous records of individual spectral data. The colors indicate the likelihood of a given spectral level in a specific frequency band. The red arrows connect the median noise level to the frequency where sperm whale clicks are omnidirectional (~ 3kHz). The 1%, 5%, 50%, 95%, 99% percentiles are shown in this order with black contour lines from the bottom upwards. The RMS is shown in magenta.

3.4.4 Variability of sperm whale propagation range

The BELLHOP sound propagation model indicated small seasonal changes in the maximum detection ranges for the low-frequency omnidirectional part of sperm whale clicks (Table 3.1). The median ambient noise levels (~53 and 57 dB re 1 μPa^2/Hz for the summer and winter respectively; see section 3.3) plus the 12 dB detection threshold, function as the thresholds at which sperm whale clicks cannot be heard and detected by the hydrophone.

The BELLHOP models showed that the propagation of the sperm whale clicks varied little with season, with the received levels dropping to the background noise levels at an average for all dives of 7 km (SD=3 km) for both winter and summer (Table 3.1). However, the winter sound propagation model showed a slightly shorter propagation range compared to the summer (in average by ~ 1 km; Table 3.1). For the clicks emitted at depths between 100 m and 750 m, the longer (by 2-6 km) detection ranges were modeled for summer. The lowest median ocean ambient sound levels at 3 kHz were also measured in summer at OSP (53 dB re 1 μPa^2/Hz).For the shallowest dive (50 m), the clicks emitted by a hypothetical sperm whale presented much shorter propagation ranges (by 8 km) in the summer. Overall, the maximum variability in detection range between seasons resulted in the more shallow dives (up to 750 m). Almost no variability was recorded on the detection distance between the seasons for the deep dives (1000 m and 1500 m).

	Propagation range [km] **(Ocean ambient sound levels [dB re 1μPa^2/Hz])**	
Whale depth	**Winter (69)**	**Summer (65)**
50	11	3
100	3	6

250	7	13
500	6	8
750	7	11
1000	4	4
1500	8	9
Average (SD)	*6.6 (2.6)*	*7.7(3.6)*

Table 3.1 - The variability of sperm whale click propagation at Ocean Station PAPA (OSP), for usual clicks (with 155 dB re 1 μPa^2/Hz source level at 3 kHz) emitted at 50, 100, 250, 500, 750, 1000 and 1500 m depth for winter and summer. The detection range of the clicks is defined by the point where the ray paths are equal or above the ambient sound levels.

3.4.5 Seasonality

A strong seasonal pattern was evident, with the highest number of sperm whale detections occurring in summer (July) and the lowest in winter (December and January) (Figure 3.7, Figure 3.10). The best loess model fit to the data (expressed as year day; span S = 0.5) (blue line in Figure 3.7) captured this seasonal pattern well (Figure 3.11) and was consistent over the sampling period. The differences in sperm whale detections among seasons were shown to be significant (Kruskal–Wallis H(3)=24.086, $p < 0.001$). Wilcoxon post hoc comparisons indicated that whale detections were significantly higher in summer (mean ± SD = 85.3 ± 11.6) than the rest of seasons (fall: mean ± SD = 66.3 ± 18.8, $p_{summer}=0.01$; spring: mean ± SD = 53 ± 15, $p_{summer}<0.001$; winter: mean ± SD = 48.2 ± 19, $p_{summer}<0.001$). Detections in winter (mean ± SD = 48.2 ± 19) were significantly lower than fall and summer ($p_{winter}=0.03$ and $p_{winter}<0.001$ respectively).

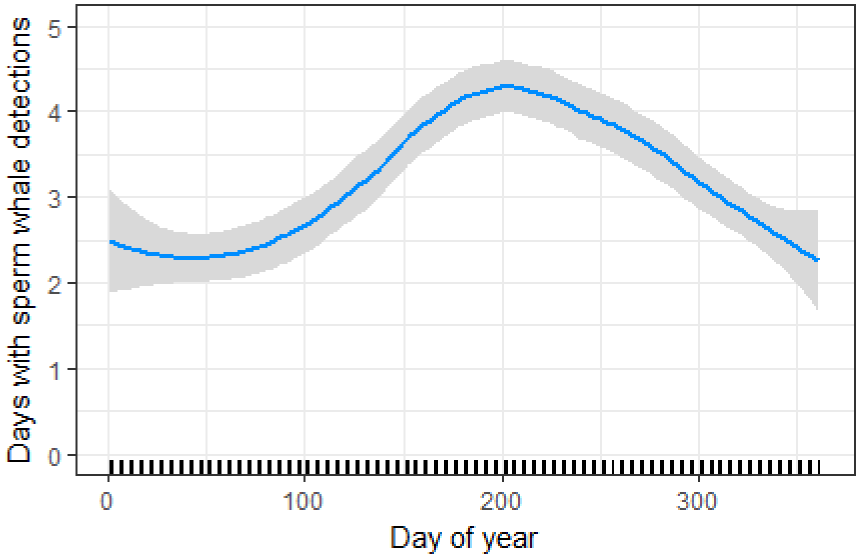

Figure 3.7 - Sperm whale presence modelled as a smooth function of the day of the year using locally weighted polynomial regression (loess). The x-axis represents 5-days bins. The expected values of whale detections (blue line), the 95% confidence band for the expected values (gray band), and a rug plot indicating where the observations occurred are shown. It indicates that sperm whale detections at Ocean Station PAPA (OSP) peak in the summer months, and decrease during the rest of the annual cycle.

3.5 Discussion

Between June 2007 and April 2012 (1605 days), the PAL was successful at detecting sperm whale presence year-round. A prominent seasonal cycle, with a 30% higher detection rate in summer compared to winter, was the dominant feature of this time series. An ambient noise analysis within the sperm whale omnidirectional vocalization frequency revealed small variability in noise levels throughout the year, providing evidence that the seasonal variation in sperm whale detections was likely not a result of seasonal changes in ambient sound levels or seasonal propagation differences. Further analysis indicated that the maximum detection range of sperm whale clicks is between 3 and 13 km for all seasons.

3.5.1 Detection performance

An acoustic monitoring program can be ineffective in identifying temporal patterns when there are variations induced by vocalization detectability (Schmidt and Pellet, 2010). Even when variation in detection probability is the rule rather than the exception (MacKenzie and Kendall 2002), it creates no bias as long as it does not show a temporal trend (Bart et al. 2004). To evaluate whether the PAL can reliably detect sperm whale daily presence, we first demonstrated that the daily probability to detect sperm whales did not vary greatly throughout the year.

This is the first time a PAL has been used to detect sperm whales. We showed that the probability of a PAL detecting sperm whale clicks on a given day was above 50% year-round. Thus, the daily presence/absence and the temporal patterns reported here likely represent natural variability related to ecological processes rather than sampling bias. Further, we showed that the probability of detecting one sperm whale producing usual clicks (ICI = 0.7) was 21%. Higher latitudes, such as the OSP region, are frequented by mature males that tend to be more solitary; the PAL was less likely to detect these whales especially if they were not foraging. Even though detections of one or two individuals were stable year-round, the presence of single males travelling through OSP was likely underestimated. However, the probability of detection increases with group size, likely resulting in more detections of foraging pods. Additionally, we showed that PAL's variable and seemingly low duty cycle did not adversely affect the temporal patterns of whale variability examined. With the sperm whales being the acoustically dominant species at OSP, there was no issue with other biological sounds exhausting the quota. Despite these potential challenges and the complex sampling strategy, we successfully detected sperm whales in 84% of the available recordings that comprised sound bites that met target signal criteria.

3.5.2 Examination of detection bias

A 4 dB difference in ambient noise levels, measured for the months with the lowest and highest detection rates within a year, can be considered very low. This supports the hypothesis that the observed seasonality in sperm whale acoustic occurrence is not a product of changes in the sound field, but rather a true reflection of presence/absence of whales. Small variability in median background noise levels at relevant frequencies allow hydrophones to detect vocal sperm whales over similar distances throughout the year. However, for a whale to be detected it must produce sounds; hence this study excludes silent individuals. With males at high latitudes spending up to 82% of their daytime foraging underwater (Jaquet et al., 2000), the missed detections are expected to be low.

The BELLHOP models showed small changes in sound propagation throughout the seasons. For all dives, the average detection range was around 7 km year-round (Table 3.1). A higher detection range (by 8 km) modeled for the 50 m dive depth in winter is a result of the mixed layer formation due to increased winds, while in the summer a strong seasonal thermocline (see companion paper, Diogou et al. submitted) leads to faster propagation attenuation and slightly shorter detection ranges. Most likely, the thermocline on the top 70 m of the water column (see companion paper, Diogou et al.

submitted) resulted in the shorter range for the shallowest (50 m) dive during the summer. Overall, the differences in measured distances (1-6 km of difference) between the seasons were variable with depth, although the difference of the averages over all depths (sperm whales start clicking soon after their dive begins) were likely negligible (1km difference between winter and summer). These predictions largely agree with previous estimates for the northeastern temperate Pacific (Barlow & Taylor, 2005).

3.5.3 Sperm whale prevalence at OSP

Even though sperm whales occur in oligotrophic and relatively unproductive waters in both the Atlantic and the Pacific Ocean (Whitehead, 2003; Wong and Whitehead, 2014), it is interesting that the OSP region, with its high-nitrate, low-chlorophyll character, can sustain a top predator year-round. In the offshore GOA, the relatively shallow permanent pycnocline (at about 100 m; Whitney & Freeland 1999a; see companion paper, Diogou et al. submitted) permits the maintenance of chlorophyll-*a* levels in winter comparable to those in summer (Boyd et al., 1995; Evans and Parslow, 1985) and allows relatively high winter primary and secondary productivity, presumably supplying sufficient food resources during all seasons.

The year-round acoustic presence of sperm whales at OSP is not surprising, given that mature sperm whales and small groups of younger males have been known to occur year-round in high latitude waters to forage and build up size and social maturity (Best, 1979; Jaquet et al., 2000; Rice, 1989; Whitehead, 1994; Whitehead and Arnbom, 1987) before their occasional, and little understood, migration to low latitude breeding grounds (Best, 1979). In contrast, females and immature whales (‘social groups’) are geographically stratified, occupying warmer tropical waters. Mixed gender social groups have been identified as far north as 50°N in the eastern North Pacific during the summer (Mizroch & Rice 2013), and codas have been recorded by a PAL moored at a different location where social groups are common (Diogou et al., submitted). However, the complete absence of codas (a typical indication of social groups) in our data indicates that social groups of sperm whales are unlikely to be present at OSP. Thus, the recorded clicks are likely from foraging 'bachelor schools' and mature males.

There was a distinct seasonal pattern in the acoustic record; detections were highest in summer and spring and lowest in winter. This pattern could represent movements of sperm whales into the area during the summer and out of the area during the winter, or an increase in foraging during the warm season, with prey aggregating groups of whales, which in turn increases the probability of detection by the PAL. During a three-year study at the same location 10 years earlier, Mellinger et al. (2004) observed a similar seasonality, although with much lower detection rates, likely associated with a lower sampling rate (1 kHz). In a low-latitude offshore location of the western North Atlantic where social groups are common, Wong & Whitehead (2014) also reported a seasonal pattern in whale detections, although their acoustic sampling only lasted through one winter and spring season. Sperm whales off east Antarctica were detected predominantly during the Austral summer (December to February) (Miller et al., 2018) while off Kaikoura, New Zealand, significant differences in the distribution of males were observed between summer and winter (Jaquet et al., 2000). More recent results from the continental slope of the western North Atlantic (35.34°N - 40.29°N) showed higher detections during the winter period (Stanistreet et al., 2018). In polar waters of the North Atlantic, sperm whales were detected only between July and January (Klinck et al., 2012).

The main driver of sperm whale occurrence is presumed to be prey availability (Jaquet and Gendron, 2002; Whitehead, 2003). An increased sperm whale presence during the summer might indicate an increased availability of food resources in the OSP region during this time. Sperm whale diet in the oceanic habitat of the GOA consists mainly of mesopelagic and bathypelagic squid (Clarke, 1980; Kawakami, 1980; Okutani and Nemoto, 1964) and some fish (Whitehead, 2003). The physical processes that enhance iron supply at OSP, a major limiting factor of phytoplankton growth in the open-ocean habitat of the GOA, stimulate primary productivity and can ultimately lead to increased availability of sperm whale prey (Boyd et al., 1996; Whitney and Robert, 2002).

In the broader OSP region, the Alaska Current and Gyre play a dominant role in the circulation and oceanography (Figure 3.1). There is a seasonal pattern in the variability of the Alaska Current and the Alaska Gyre with changes in magnitude and position (Crawford et al., 2007). In winter, the Alaska Current intensifies causing the locations of the divergence of the North Pacific Current and the Subarctic Frontal Zone to move south (Figure 3.1A); the opposite takes place in summer (Figure 3.1B) with a latitudinal maximum in July-August (Crawford et al., 2007). The North Pacific Transition Zone moves with the same seasonal pattern (Figure 3.1). Thus, the authors hypothesize that the northern displacement of the Subarctic Frontal Zone and the Transition Zone can influence sperm whale occurrence at OSP by increasing water mixing, and transporting nutrients and organisms closer to that region (Polovina et al., 2015). Strong seasonal patterns, similar to that of sperm whale acoustic occurrence, have been observed in the occurrence of their prey species near

OSP. Specifically, neon flying squid (*Ommastrephes bartramii*), part of the sperm whale diet (Kawakami, 1980), perform regular seasonal movements to the subarctic frontal zone in early summer, with the largest females moving further north into the area of OSP (50°N between 165°W and 130°W) (Kubodera et al., 1983). At OSP, they are typically found in the top 100 m of the water column (Murata, 1988), perhaps facilitating prime foraging conditions for sperm whales. Sperm whales are historically known to concentrate in large-scale frontal areas (ca. 40°N – 43°N) (Mizroch and Rice, 2013), together with a variety of marine top predators, from seabirds to sea turtles, sharks, tuna and elephant seals (Block et al., 2011; Kappes et al., 2010; Saijo et al., 2017). Hence, the seasonality in sperm whale occurrence at OSP is likely reflecting (through a series of food web interactions) the shifts in productivity and biomass levels defined largely by the seasonal oscillations of the Subarctic Frontal and Transition Zone.

The occurrence of sperm whales in the open ocean is expected to be largely defined by oceanography (Gannier and Praca, 2007; Pirotta et al., 2011) and bathymetry. Even if OSP is largely characterized by low bathymetric complexity (Yen et al., 2005), some deep seamounts (e.g. the Pathfinder Seamount: 500-4000m depth, ~136 km from OSP, Figure 3.8) are scattered in the wider area. Seamounts are globally known to aggregate squid and sperm whales (Hann et al., 2016; Jaquet and Whitehead, 1996; Pitcher et al., 2007; Waring and Hamazaki, 2001) and their presence in the wider region likely contributes in making the area around OSP into an optimal foraging habitat of the open ocean in the GOA.

3.5.4 Detection of other species

Overall, as the vocalization rate increases, the probability for sperm whales to be detected by the PAL increases as well. For the same reason, other species that produce long calls and calling bouts, with short ICIs have better a probability of being detected (Miksis-Olds et al. 2010, Denes et al. 2014). In this study, at least six more cetacean species were detected. Cuvier's (*Ziphius cavirostris*), Baird's (*Berardius bairdii*), and Stejneger's (*Mesoplodon stejnegeri*) beaked whales were detected coincidentally with sperm whale calls, but their presence could be anticipated since they are known to have similar habitat and prey preferences as sperm whales. In addition, a number of humpback whale (*Megaptera novaeangliae*), killer whale (*Orcinus orca*), Pacific white sided dolphin (*Lagenorhynchus obliquidens*), and other unidentified delphinid vocalizations were registered, predominantly between spring and fall. The almost constant acoustic presence of sperm whales throughout the deployment period often exhausted the available daily quota of sound bites early in the day. Therefore, the majority of the additional species were coincidentally detected with sperm whale calls, obscuring robust data on temporal occurrence patterns for these species. Killer whales were an exception due to their high probability to be detected by the PAL (Miksis-Olds et al., 2010), and their detections at OSP could be considered to reflect true temporal patterns of the more vocal ecotypes. The abundance of species detected indicates a high level of cetacean diversity at OSP, and emphasizes the importance of this open-ocean habitat for a variety of apex predators. Future applications of a PAL to monitor an entire cetacean community or other less common species will require adjustments to the triggering criteria to increase the species detected in a deployment area.

The PAL has proven to be a reliable and highly efficient tool for assessing the daily presence of species that vocalize frequently, such as the sperm whale, at an inaccessible offshore location. The study area, located south of the Temporary Maritime Activities Area (Figure 3.1), is of interest to the U.S. Navy. The year-round presence of sperm whales and other threatened deep-diving cetaceans at OSP, emphasize the areas' importance as a potential critical habitat for the species. With the sperm whales spending the entire year at the OSP area, this offshore site represents a preferred foraging site for what is believed to be male animals. There is need for continuation of acoustic sampling at OSP and expansion of passive acoustic monitoring to other stations of Line P or the Ocean SITES Network, where cetacean occurrence can be paired with invaluable *in situ* measurements and offer a comprehensive picture of the ecosystem.

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3.7 Appendix

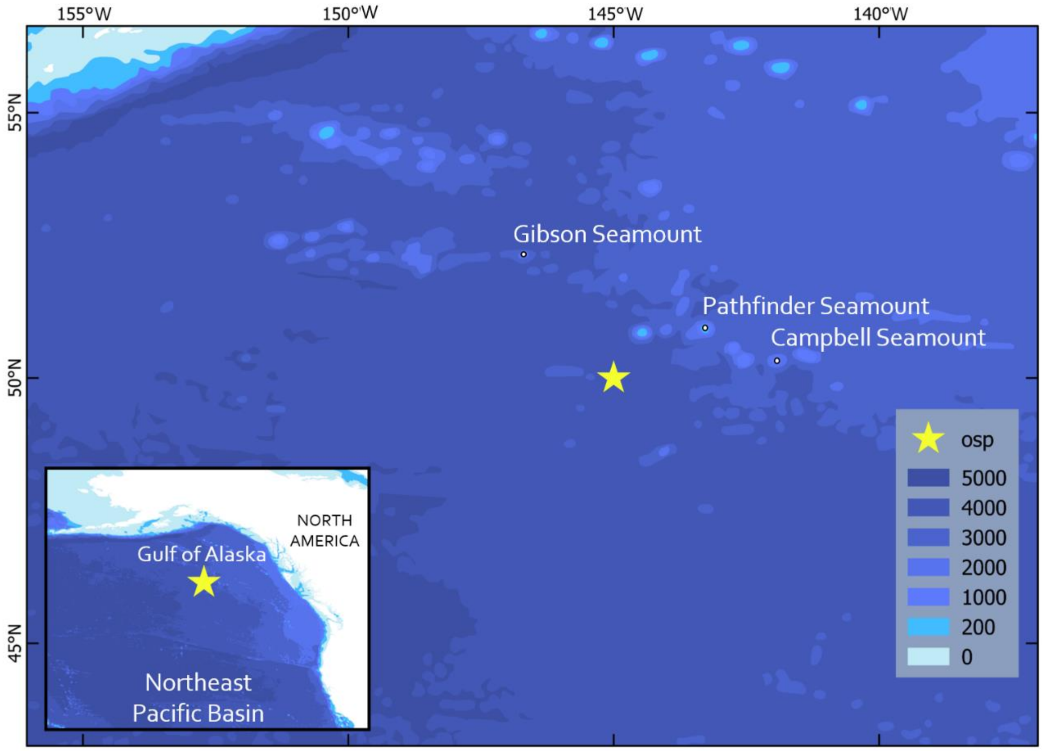

Figure 3.8 - Bathymetric map of the broader study area with the deployment location of the Passive Acoustic Listener (PAL) at Ocean Station PAPA (OSP). The Pathfinder, Campbell, and Gibson Seamounts nearby are also indicated. The position of OSP in relation to the wider Northeast Pacific Basin is shown in the bottom left frame. The color codes for the different depths (in meters) is shown in the bottom right frame.

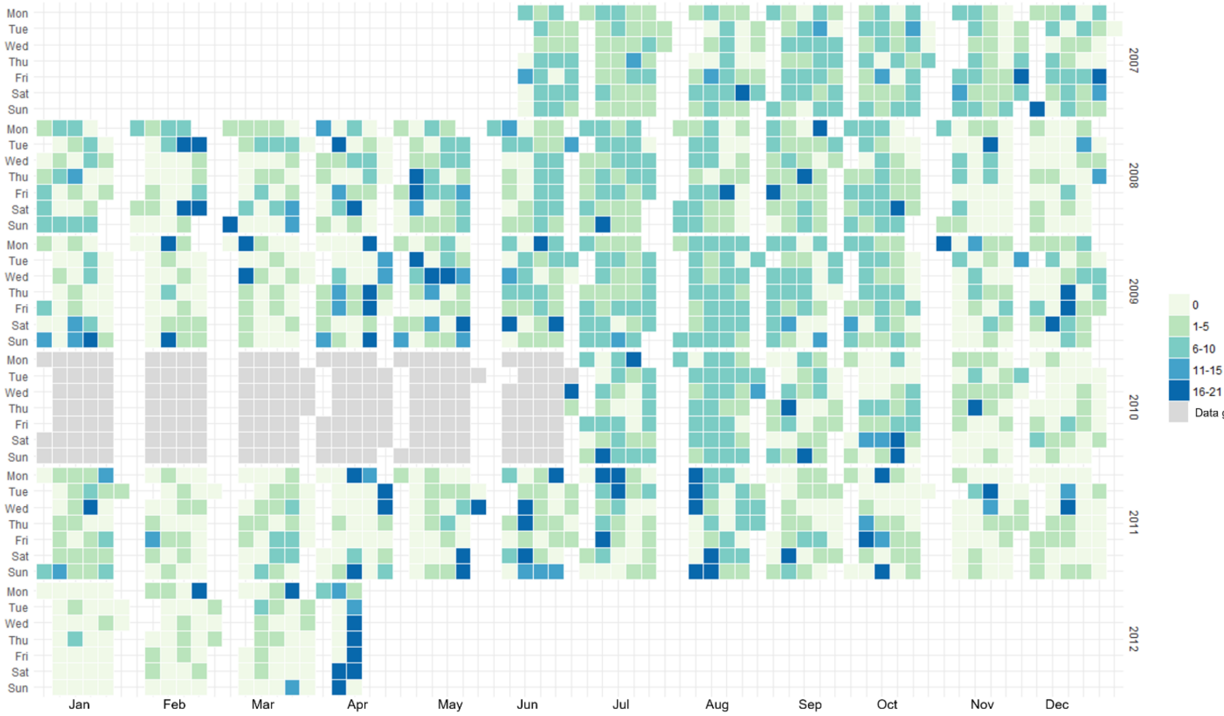

Figure 3.9- Number of sound bites with sperm whale acoustic detections per day, at the Ocean Station PAPA (OSP) throughout the sampling period, June 2007 until April 2012. A data gap, due to due to delayed maintenance of the mooring, is shaded in grey. The

empty cells between the months do not represent sampling days, they function as a month separators.

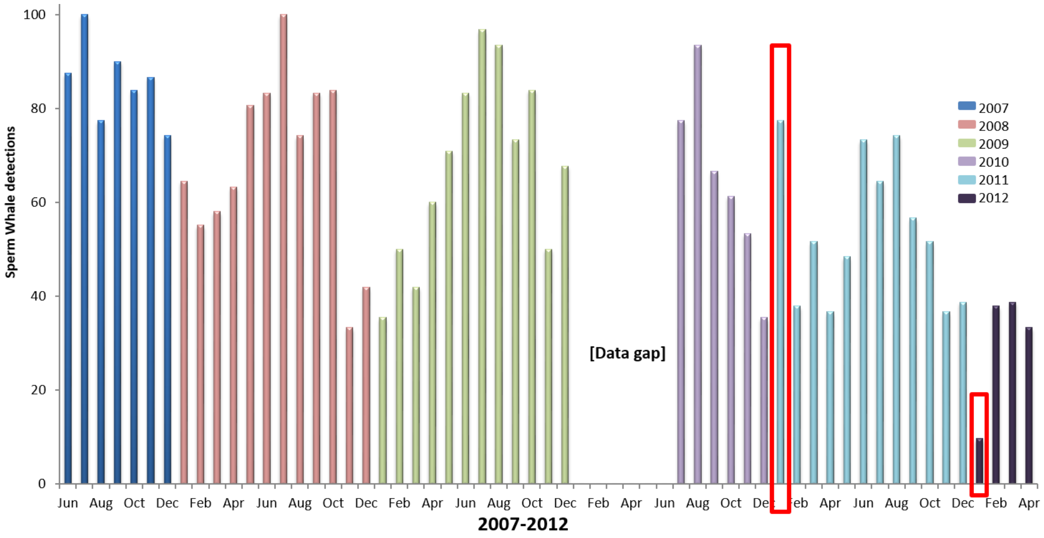

Figure 3.10 - Time series of acoustic detections of sperm whales (*Physeter macrocephalus*) at OSP. The y axis represents the percentage of days with detections per month during the period June 2007 - April 2012, standardized for effort. There was a data gap from 1 January to 15 June 2010. The different years are represented by different colors. The red frames emphasize on the anomalous detections recorded in January 2011 and January 2012.

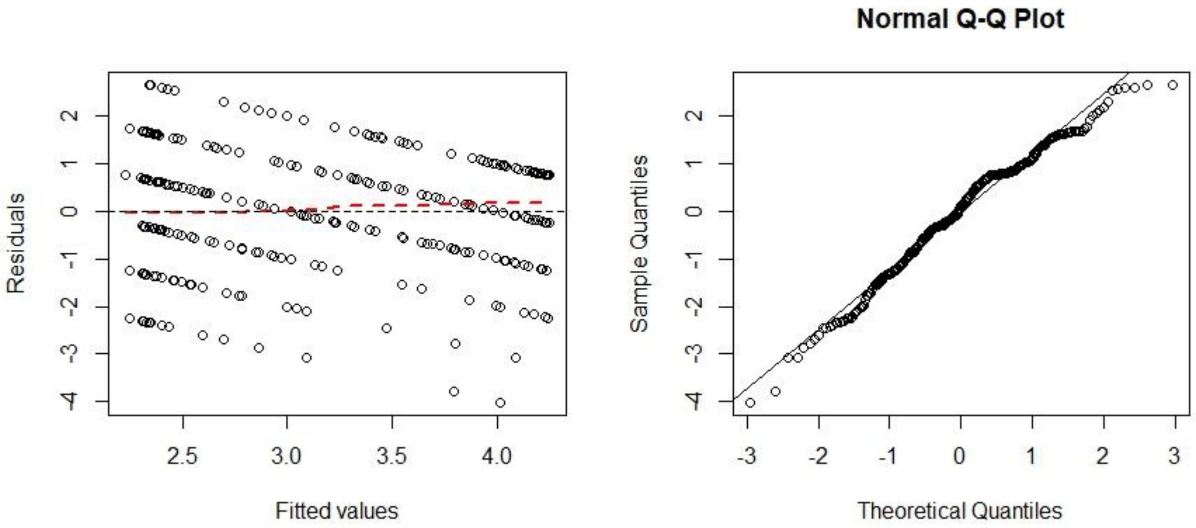

Figure 3.11 - The graphical diagnostics for the loess model: residuals against fitted values (left plot) showing a reasonably good fit and constant error variance (red dashed line: loess fit to the residuals), and quantile-quantile (Q-Q) plot (right plot) indicating normality of distribution.

4. Sperm whale (*Physeter macrocephalus*) acoustic ecology at Ocean Station PAPA in the Gulf of Alaska – Part 2: oceanographic drivers of interannual variability

Everyone curses the sea but it is the wind to blame

Όλοι βρίζουν την θάλασσαν, ενώ πταίει ο άνεμος.

—Dimitrios Kambouroglou

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4.1 Abstract

Understanding top predator responses to environmental variability is key to assessing potential impacts of global warming on marine ecosystems. However, tracking environmental changes and their effects across multiple trophic levels up to predators can be difficult. Here, we related the interannual (2007-2012) acoustic occurrence of sperm whales (*Physeter macrocephalus*) at Ocean Station PAPA (OSP), in the offshore Gulf of Alaska (GOA), to environmental drivers within an explicit time-series modeling framework. In a model based on a combination of *in-situ* and remotely sensed variables, ocean heat content (HC), meridional current (V), eddy kinetic energy (EKE), strength of the permanent pycnocline (maxBVF), sea surface temperature (SST) and SST standard deviation (SSTsd) explained 51% of the variability in sperm whale presence, indicating a positive relationship between sperm whale occurrence and increased ocean heating, vertical stratification, and circulation. Sperm whale detections were anomalously high in summer 2010 and winter 2011, and anomalously low at the end of summer and winter 2008, and spring 2011. Results suggest these strongly anomalous detection events reflect a response to El Niño–Southern Oscillation (ENSO) events, with an 8-month lag. In the study area, El Niño leads to a stronger permanent pycnocline, a weakening of the Alaska Gyre, a northward expansion of the North Pacific Subarctic Frontal Zone, and a prevalence of offshore mesoscale eddies, likely favoring the abundance of squid and their predator, the sperm whale. The overall results are consistent with a scenario of increasing sperm whale occurrence at high latitudes under increased ocean warming.

4.2 Introduction

Quantifying a species' habitat preferences is key for understanding its ecology. Knowledge of the environmental characteristics associated with a species preferred habitat can help scientists identify environmental shifts through changes in its distribution and abundance (Gregr et al., 2013). In addition, such knowledge can also inform predictions of changes in a species distribution caused by changes in the environment, for example associated with a changing climate. To quantify environmental and ecological changes in the oceans, long-term measurements are required. Sperm whales (*Physeter macrocephalus)* are mesopelagic apex predators and are considered ecosystem sentinels (Bossart, 2006; Moore and Huntington, 2008). They are listed as 'Vulnerable' under the International Union for the Conservation of Nature (IUCN) criteria, 'Endangered' under the United States (USA) Endangered Species Act, and 'Depleted' under the US Marine Mammal Protection Act (MMPA; NMFS 2013). An improved understanding of the ecological processes that determine their abundance and distribution can be used to inform management and conservation decisions. However, information on habitat preferences or interannual variability in the occurrence patterns of this deep-diving species are sparse (Jaquet and Gendron, 2002; Rendell et al., 2004), and their critical habitats remain largely unidentified.

Technological advancements of autonomous passive acoustic recorders permit the acquisition of long time series of cetacean vocalizations in a non-invasive manner (e.g. Mellinger et al. 2004, Moore et al. 2006). These can be used in combination with statistical modeling techniques to quantify the relationship between animals and their environment (Stafford et al., 2009). However, to date only a few studies have explicitly used time series analysis and seasonally adjusted methods to characterize the temporal variability in occurrence of marine mammal species and their responses to changing environmental conditions (Trites and Antonelis, 1994; Stafford et al., 2001). The majority of these approaches, by necessity, relied on remotely sensed environmental measurements since *in situ* data at an adequate sampling resolution are rare – especially for far offshore areas (Burtenshaw et al., 2004). Studies exploring the relationship between sperm whales and their environment have often used static variables such as seafloor topography, which is relatively easy to obtain (de Stephanis et al., 2008; Praca et al., 2009; Pirotta et al., 2011). Deep areas close to the continental shelf break with steep bathymetric features, as well as remote seamounts, have been identified as prime sperm whale habitat (Jaquet and Whitehead, 1996; Waring and Hamazaki, 2001; Drouot et al., 2004; Pirotta et al., 2011; Hann et al., 2016). Bathymetric features are thought to induce vertical water circulation and a redistribution of nutrient supply across the water column which leads to an aggregation of sperm whale prey (e.g. Biggs et al. 2000, Praca et al. 2009).

A major factor influencing cetacean presence and movements is food availability (Gregr et al., 2013; Palacios et al., 2013). While we are now able to obtain long-term records of cetacean occurrence patterns using acoustic monitoring, we often lack equivalent occurrence records of their prey. Determining actual squid (the sperm whales' primary prey item; Okutani & Nemoto 1964, Clarke 1980) abundance and distribution is difficult. Catch information obtained by the fishing industry typically does not provide the required spatiotemporal resolution. Hence, when modeling cetacean habitat preferences we often rely on abiotic and biotic variables that are considered drivers of ocean productivity and consequently of prey aggregation (Gregr et al. 2013, Palacios et al. 2013).

The deep-ocean pelagic food web is a complex ecosystem, with highly dynamic interactions influenced by a range of biological and geophysical variables (Longhurst, 2007). The offshore marine environment is typically characterized by phytoplankton consisting of small diatoms that export small amounts of carbon to other organisms and require more steps for energy to reach the higher trophic levels. Therefore, in the open ocean the connection from ocean physics and primary productivity to top predators is even more tenuous (Miller and Wheeler, 2012). Capturing and explaining potential responses of cetaceans to environmental changes has been more successful with species of baleen whales (Stafford et al., 2009; Zerbini et al., 2015; Thomisch et al., 2016) that feed on the lower trophic levels where the trophic distance between predator and prey is shorter (Renner et al., 2012). In contrast, sperm whales have evolved to forage in the deep-ocean environment and are separated from the near-surface food chain due to their mesopelagic feeding habitat, which makes relations between physical forcing and high trophic levels more challenging to assess. To accomplish this, physical and biological measurements over long temporal scales and throughout the entire water column are required (Redfern et al., 2006).

Located in the subarctic North Pacific, Ocean Station PAPA (hereafter referred to as OSP) is a deep-ocean observatory that collects a wide variety of high-resolution water column measurements (Harrison, 2002; Freeland, 2007). OSP provides one of the longest oceanographic time series in the world and provides valuable data on the environmental conditions in the central Gulf of Alaska. Even after 60 years of continuous recording of the physical oceanic conditions at OSP, most studies have focused on the lower trophic levels (e.g. Boyd et al. 1995, Boyd & Harrison 1999, Peña et al. 2007), while studies on higher trophic levels, including cetaceans, have received far less attention.

Mellinger et al. (2004) and Diogou et al. (see companion paper; submitted) used passive acoustics to detect sperm whales at OSP and characterize their seasonal presence. Thus far, however, there has been no attempt to link sperm whale occurrence patterns to the environmental conditions at the seasonal and interannual scales in that region.

In this study, we related sperm whale acoustic occurrence to the interannual variation in a suite of oceanographic variables that influence biological productivity, using a time-series-based statistical modeling framework. We considered both *in situ* and remotely sensed variables, and explored models that considered them both together and separately. The goal was to facilitate future studies seeking to predict sperm whale distribution, providing practical options to researchers that have different data sources available.

4.3 Materials and Methods

4.3.1 Study area

Our study area is centered around OSP, located at 50°N and 145°W in 4200 m deep water and 913 km offshore (Whitney and Freeland, 1999). OSP is the most offshore station of a network of 26 oceanographic survey locations known as Line P which extends from the Strait of Juan de Fuca to OSP (Figure 4.1). The study area's oceanography is defined by its location south of the Alaska Gyre (Dodimead et al., 1963) in the subarctic Pacific. The gyral circulation pattern (Figure 4.1) leads to upwelling at the center of the gyre (Xie and Hsieh, 1995) and downwelling along the gyre boundaries (Okkonen et al., 2001). Additionally, the northeastern subarctic Pacific is one of the major high-nitrate, low-chlorophyll regions in the world's oceans (Longhurst, 2007).

Phytoplankton growth is limited by light and iron during the winter (Maldonado and Price, 1999), when storms deepen the mixed layer (Whitney and Freeland, 1999). In spring, increasing light and temperatures stimulate primary productivity. The mixed layer reaches its minimum depth by the end of summer, and during this time lowest nutrient levels (nitrate and silicate) are observed (Whitney and Freeland, 1999). There is no evidence of regular spring or summer blooms in the vicinity of OSP (Parsons and Lalli, 1988). The water stratification at OSP consists of a shallow (up to 100 m) seasonal pycnocline, a deep (about 100-250 m) permanent pycnocline, and a deep layer (below 1000 m) where temperature is fairly stable and salinity increases slowly (Dodimead et al., 1963). There is a strong relationship between the two pycnoclines and the mixed layer depth: in the summer, the base of the mixed layer is underlined by the seasonal pycnocline and from fall until early spring by the top of the permanent pycnocline (Steele et al., 2010). Comprehensive reviews of the oceanographic characteristics at OSP are presented in Harrison (2002) and Freeland (2007).

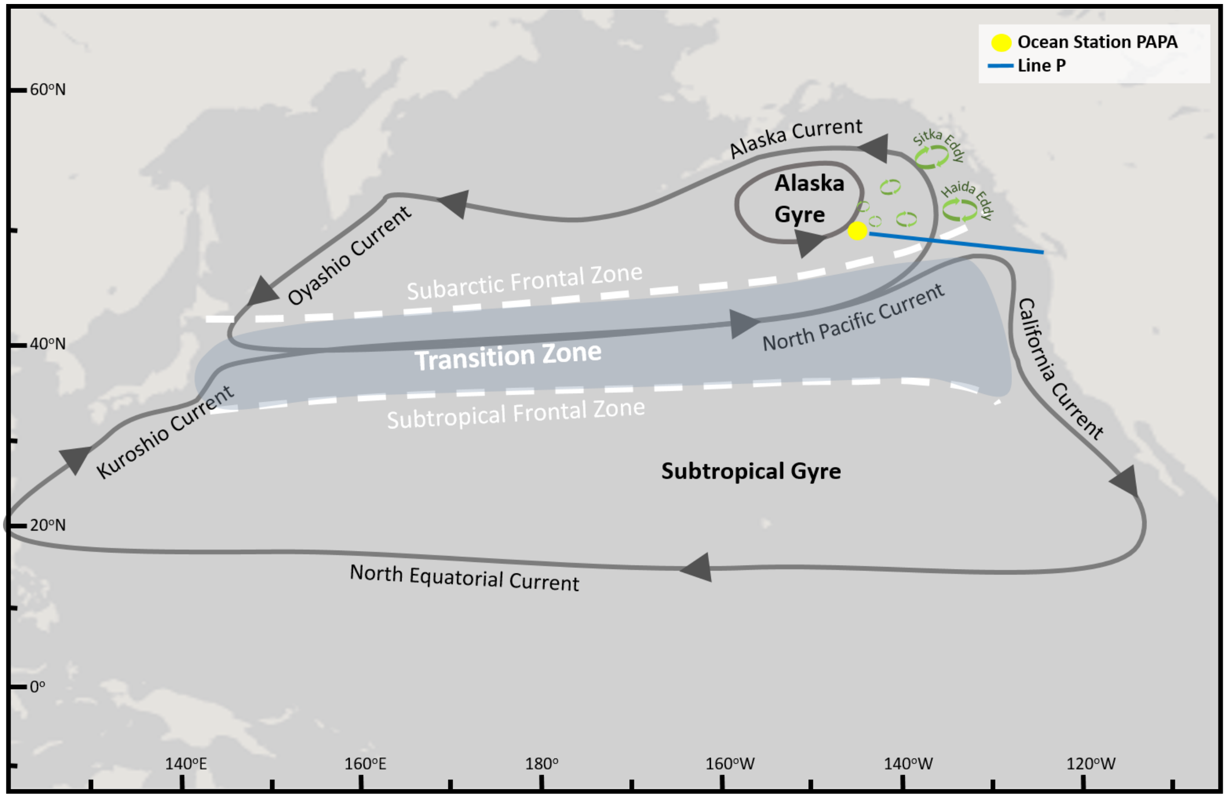

Figure 4.1 - Location of the Ocean Station PAPA (OSP) buoy (yellow circle) where the Passive Aquatic Listener (PAL) was deployed and the acoustic sampling was carried out, and the Line P program where long oceanographic time series have been collected (blue line). The gyral circulation of the North Pacific and particularly the Gulf of Alaska are indicated (map was adapted and redrawn principally from Block et al. 2011 and also Pearcy, 1991; Tomczak & Godfrey, 2001; Whitney et al., 2005).

4.3.2 Data Collection

4.3.2.1 *Acoustic data*

To investigate sperm whale acoustic occurrence at OSP we used recordings from a Passive Aquatic Listener (PAL) (Nystuen, 1998; Anagnostou et al., 2011) deployed at a depth of 190 m and operated between 2007 to 2012. The PAL's sampling strategy included ‘waking up’ from a sleep mode every 5 min and listening for 4.5 s at 100 kHz sampling frequency. This way, PAL functioned at a maximum 1.5% duty cycle ensuring the daily detection of highly vocal odontocete species such as sperm whales. Extensive description of the instrumentation, sampling regime, data analysis and results, is presented in detail in Diogou et al. (see companion paper; submitted).

PAL collected acoustic clips of 4.5-s duration each; are called sound bites and up to 21 of them could be stored in a day when a real-time event detector identified non-stationary (transient) signals, including sperm whale clicks. Sound bites were the original sampling unit and were all analyzed for presence or absence of sperm whale acoustic signals. If at least one sound bite in a given day included sperm whale clicks, we recorded daily presence. Ultimately, the response variable was recorded as the number of days with confirmed sperm whale presence in a 5-day bin. The 5-day bin was selected as a compromise between the instrument’s high sampling resolution and the need to combine multiple days of remote sensing data in order to obtain a valid environmental measurement due to cloud cover and other sources of gappyness. The raw response was a discrete variable in units of days with sperm whale presence per 5-day bin, taking values from zero to five.

4.3.2.2 *Oceanographic data*

Thirteen oceanographic variables were collected and used for the analysis (Table 4.1). Eight variables were measured or calculated by *in situ* instruments and five through remote sensing. Time series for both the *in situ* and remotely sensed variables were extracted for a period starting six months prior to the acoustic sampling (in order to allow the computation of temporal lags) and ending on the same day of the acoustic sampling.

In situ variables

Daily measurements of eight variables describing near-surface currents, ocean heat content, and water-column stratification variables were extracted and 5-day averages were computed for each one. All *in situ* data were downloaded from the NOAA Ocean Climate Stations website (OCS, http://www.pmel.noaa.gov/ocs) for OSP for the period 1 January 2007 - 29 April 2012.

Four variables describing near-surface currents were extracted for the 35-m depth. This depth offered a time series with the fewest amount of missing values while maintaining the deepest measurement. The magnitude of zonal (U) and meridional (V) current components, current speed (S), and current direction (D) were used for analysis.

Ocean heat content (HC) was calculated by vertically integrating temperatures over the 1 – 300 m (the maximum depth of measurements) range in the water column. The discrete temperature measurements were imported into the software Ocean Data View (ODV, Schlitzer 2016) to extract interpolated values at 1-m depth intervals within the upper 300 m. HC was calculated using the following formula (Pickard and Emery, 1990; Dijkstra, 2008):

$$HC = \mathrm{Cp} * \rho * \int_h^0 \mathrm{T(z)dz}, \quad \mathrm{in}\,\frac{\mathrm{J}}{\mathrm{m}^2} \quad [1]$$

Where Cp is the specific heat of seawater, ρ is the mean density of seawater, and h is a chosen depth (300 m) across which there is minimal heat transfer. T(z) is the temperature at each depth interval dz. Heat Content (HC) is a measure of the heat stored within the upper 300 m of the ocean.

We used the temperature and salinity profile measurements for the upper 200 m to compute the Brunt–Väisälä Frequency (BVF), or buoyancy frequency, of the water column as a measure of strength of stratification and stability (Pickard & Emery 1990). BVF controls the mixing and the vertical transport of nutrients and other particles between nutrient-rich deep waters and the sunlit surface waters (Miller and Wheeler, 2012). The temperature and salinity measurements were imported into ODV to calculate the BVF using 1-m interpolated values. To separate the two stratified layers (seasonal and permanent pycnoclines) found in the study area, we divided the water column into two parts. The depth separator was set at 81 m for most cases, and manually adjusted to a different depth during times with anomalous BVF values to ensure a clear separation of the two pycnoclines (Figure 4.2). With the ODV 'iso-surface' tool, we extracted the maximum BVF value and the corresponding depth for each layer. The depth of the highest BVF value corresponded to the pycnocline in the respective layer. Three variables were derived from this result: the integrated BVF values for the 0-75 m layer (intBVF75), fully encompassing the shallow seasonal pycnocline, and the depth (ZmaxBVF) and strength (maxBVF) of the permanent pycnocline for the 81-100 m layer. The 75 m and 81 m depths were chosen to ensure that the two pycnoclines were well separated without observations from the deep pycnocline being included in the calculations of the shallow pycnocline.

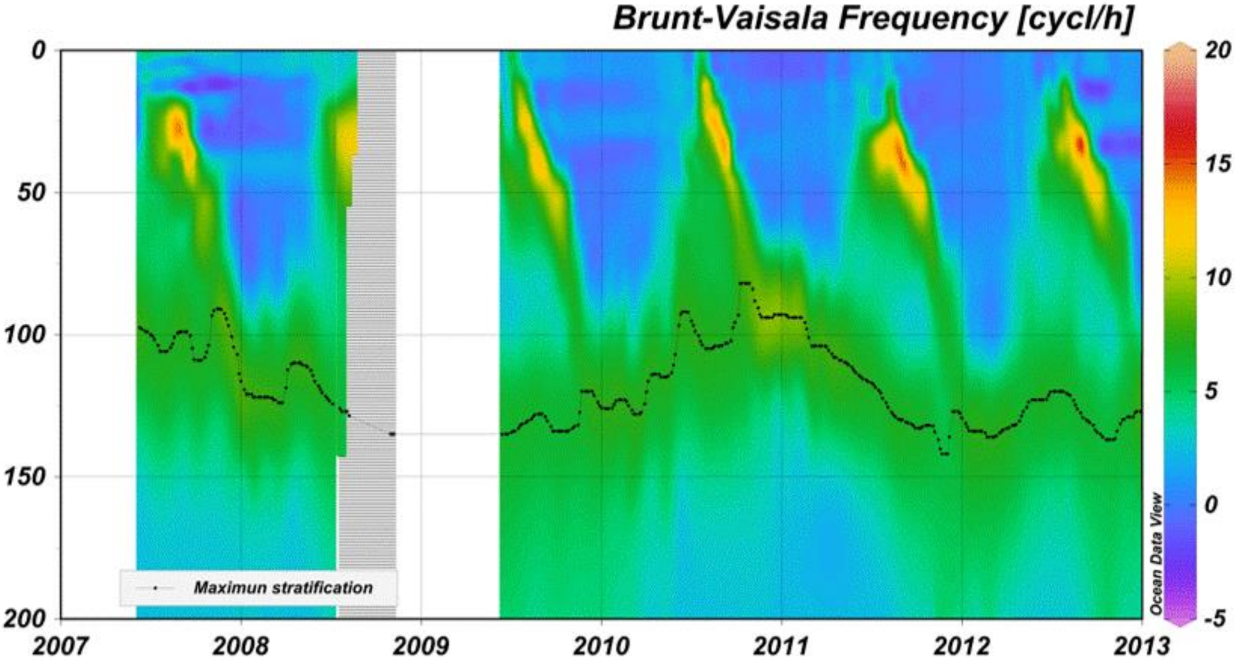

Figure 4.2 - Time series of Brunt–Väisälä frequency (color shading) in the top 200 m of the water-column at Ocean Station PAPA (OSP). The two pycnoclines are evident, with the shallow one seasonally extending from the surface to about 75 m depth and the deep permanent one traced by the black line around 100-130 m.

Remotely sensed data

In addition to the *in-situ* environmental data available from the OSP mooring, we extracted satellite remote sensing data in a 1 x 1 degree box (about 111 × 85 km in longitude and latitude, respectively) centered at OSP for the period 1 January 2007 to 17 April 2012. For data that were available at daily resolution, the mean was computed for all grid cells inside the box and then averaged into 5-day bins. Variables provided as 8-day rolling averages were matched with the closest dates of the 5-day means of the sperm whale acoustic occurrence data. The following remotely sensed variables were downloaded directly from the ERDDAP website (http://coastwatch.pfeg.noaa.gov/erddap/index.html) (Simons, 2016):

Ekman Upwelling (WUP) in the open ocean, was computed from 'Wind Stress, QuikSCAT SeaWinds, 0.25°, Global, Science Quality (8-day average)' (NASA/JPL,) (2007-2009), and 'Wind Stress, Metop-A ASCAT, 0.25°, Global, Near Real Time (8-day average)' (NOAA/NESDIS,) (2009-2012). Sea surface temperature (SST) measurements corresponded to 8-day composite data (Aqua/MODIS,). The standard deviation of SST (SSTsd) within the 1x1-degree box was computed as an indication of the presence of thermal fronts that function as biochemical hotspots (Zainuddin et al., 2008). Chlorophyll-*a* concentration (CHL) was used as a proxy for phytoplankton biomass in the ocean surface. We used 8-day composite Chlorophyll-*a* data (Aqua/MODIS,). Eddy kinetic energy (EKE), an indicator of mesoscale (eddies, meanders) activity in the ocean, was calculated from satellite altimetry measurements of sea surface height anomaly available from the Aviso website (http:/www.aviso.oceanobs.com/duacs). EKE fields (in cm^2/s^2) were computed for each AVISO map using MSLA geostrophic velocity anomalies (merged measurements from four altimeters: Jason-1, ENVISAT, GFO and Topex/Poseidon), following the equation in Ducet et al. (2000):

$$\text{EKE} = \frac{1}{2} * (u^2 + v^2) \quad [2]$$

Where u = zonal geostrophic currents, v = meridional currents.

4.3.2.3 *Climate indices*

The Oceanic Niño Index (ONI) was used to identify El Niño and La Niña events in the tropical Pacific. Event detection was based on anomalies identified in the SST time series provided for the Niño 3.4 region (5°N-5°S, 120°-170°W) (NOAA Climate Prediction Center, 2017). The Pacific Decadal Oscillation (PDO) index time series (Mantua, 2017) was also examined and was used for providing context and interpretation.

4.3.3 Data analysis

4.3.3.1 *Time series analysis rationale*

Time series of both whale detections and oceanographic measurements contained three main signals and scales of variability: *seasonal*, defined as a repeating pattern within a fixed period; *trend*, defined as a long-term (over one or several years) increase or decrease in the data; and *irregular*, defined as oscillations with irregular rises and falls. The seasonal and trend components are often prominent signals in a wide variety of variables that may be conceptually unrelated to each other and that can produce spurious regression effects (Hassler, 2003; Jeffrey and Wooldridge, J., 2011). The irregular component describes variation not explained by trend or seasonality (Cleveland and Terpenning, 1982) and, in our study, is thought to contain information on the low-frequency interannual variability. In addition, random noise (random errors) often includes high-frequency variability that may obscure the signal of interest (Chatfield, 2004). We followed the process described below and illustrated conceptually in Figure 4.3, to remove three components (trend, seasonal, and noise) and isolate the irregular signal associated with the interannual variability (Chatfield, 2004).

The seasonal (periodic) component was estimated by applying a locally weighted regression fit (loess) (Cleveland et al. 1992) on the day of the year centered on each 5-day bin of the sperm whale detection time series (with values between 1 and 365; following Zuur et al., 2009) The seasonal component, estimated in the companion paper of Diogou et al. (see companion paper; submitted), was subtracted from the raw time series resulting in the seasonally adjusted (i.e., de-seasonalized) time series. In a second step, any trend in the data was removed (i.e, de-trended) by subtracting the fitted values of a linear model from the de-seasonalized series. We applied a running Savitzky Golay cubic smoothing filter estimated over five points (each point being a 5-day bin) to remove the high-frequency noise, smooth out irregular roughness of the random noise, and to enhance the low-frequency interannual pattern. We applied these adjustments to both response and explanatory variables (Figure 4.3). The residual (i.e., 'anomaly') time series represented the underlying interannual signal that was formally modeled. This interannual signal was punctuated by several strongly anomalous events (Figure 4.4) that we interpreted more informally in the context of large-scale interannual variability and related them to basin-scale climate indices (ONI, PDO).

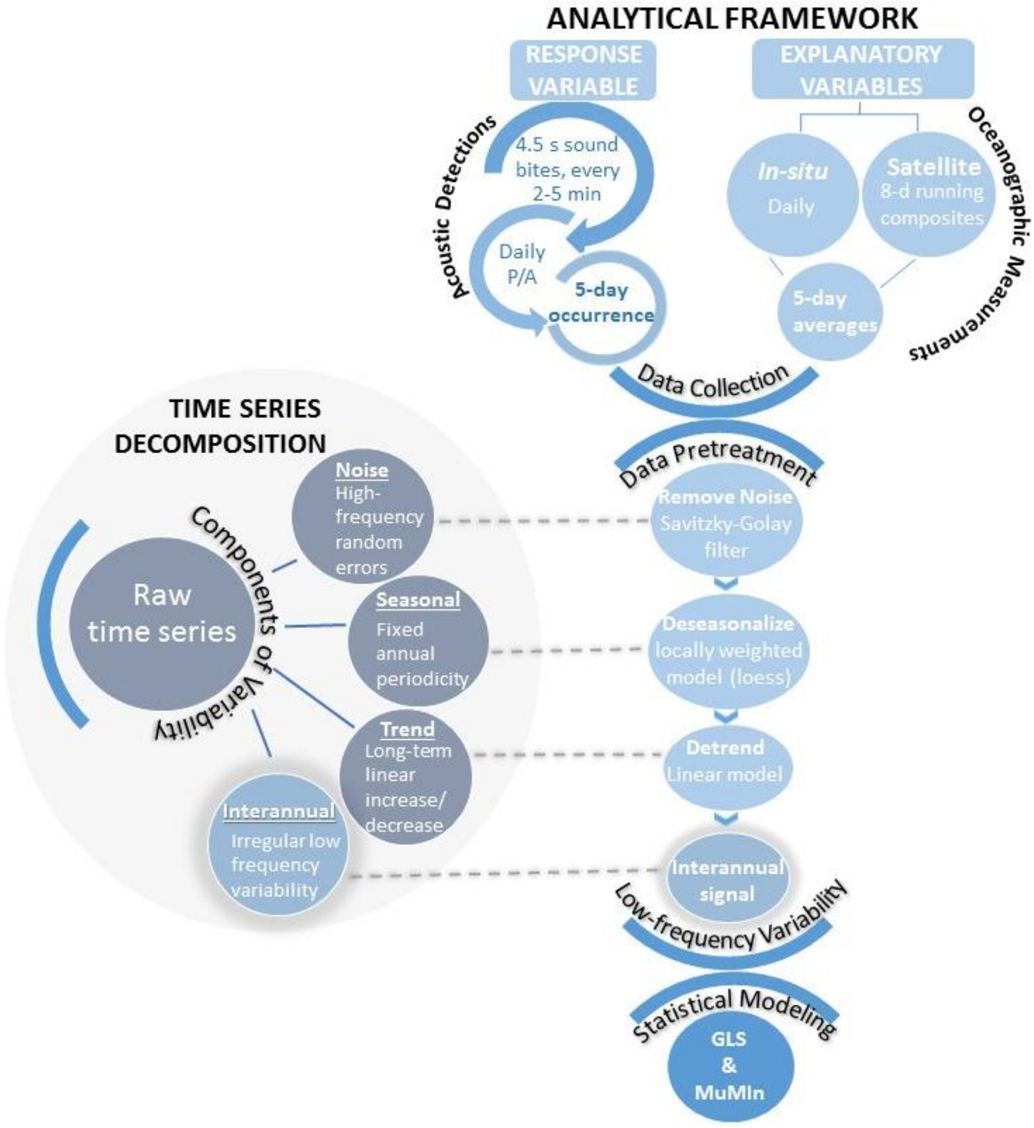

Figure 4.3 - Summary of the time series analysis rationale with the main signal components, what they represent and how they were treated.

4.3.3.2 *Multicollinearity and lagged responses*

Multicollinearity (Zuur et al., 2009) was assessed using the variance inflation factor (VIF), in the 'faraway' R package (Faraway, 2016), and applied to the full set of explanatory variables. Variables with a VIF value greater than 4 were included in a stepwise process to reduce multicollinearity by removing variables and thus reduce VIF scores (Zuur et al., 2010). Scatterplot matrices were used to assist in determining which variables to exclude by identifying high collinearity in pairs of predictors and the level of correlation with the response variable. In cases where collinearity within pairs was evident, the predictors that correlated least with sperm whale occurrence was removed before fitting the models.

We examined cross-correlation function (CCF) plots of each explanatory variable and the response and tested for correlations for lags of up to 2 months (12 lags) (as was done in Wong & Whitehead 2014) to identify the appropriate lag for each explanatory variable. The lags chosen represented the highest significant lag with the explanatory variable leading the response.

4.3.3.3 *Model specification and selection*

Models were built within a generalized least squares (GLS) framework, using the ‘nlme’ R package (Pinheiro et al. 2015) to characterize the relationship between presence of sperm whales and environmental conditions. GLS models allowed us to account for and correct temporal correlation structure among residuals in a regression model (Pinheiro and Bates, 2000). Autocorrelation function (ACF) and partial autocorrelation function (PACF) plots of the global model’s (includes all the variables to be tested for relationships) residuals were inspected to determine any temporal correlation structure. The structure identified (Autoregressive Moving Average, ARMA: p, q) by the ACF and PACF analysis was added as a factor in the GLS global model with the function corARMA from the ‘nlme’ package (Pinheiro J et al., 2015).

The multi-model inference ‘MuMIn’ R package (Barton, 2018) was used for model selection. Using the global model as a foundation, the ‘dredge’ function was used to build all possible model combinations and to rank them according to the Akaike Information Criterion for small samples (AICc). We picked the best-ranked parsimonious model from all possible models according to their AICc difference to the minimum AICc score (ΔAICc = 0) (Burnham et al., 2011). We further examined the relative importance of individual variables in the global model by applying the function ‘importance’ (sum of 'Akaike weights' over all models including the explanatory variable; Barton, 2018) on the table of models produced. Important variables were interpreted as evidence that the oceanographic variable explained the sperm whale presence. The goodness-of-fit for the best models was assessed with the function ‘r.squaredLR’ (Barton, 2018) to provide an estimation of the variance explained by the GLS models.

The R package ‘car’ (Fox et al., 2011) was used for diagnostic purposes on both the global model (with all the variables to be tested for relationships) and the best model (parsimonious with the most significant variables and lowest AICc score). Model residuals were evaluated for heterogeneity and over-dispersion (Ramsey and Schafer, 2002), based on diagnostics from quantile-quantile (Q-Q) plots, and plots of residuals versus fitted values. After the global models including the correlation structure were fit and the best models selected, we checked for non-zero autocorrelation in the errors using ACF and PACF plots on the best models’ residuals to ensure the model adequately addressed any temporal correlation.

The whole process described was repeated three times, once for each of the data sets that considered: a) a combination of *in situ* and remotely sensed variables, producing the ‘full model’ (FULL); b) only *in situ* variables, producing the ‘*in situ* model’ (IS); and c) only remotely sensed variables, producing the ‘remote sense model’ (RS). We only considered the 5-day bins that included both *in situ* and remotely sensed measurements; samples with missing data were excluded from modeling. We provided three categories of models (FULL, IS, and RS) allowing the comparison (using AIC) of the predictive ability of the different data sources, and providing options to researchers with access to different types of data sources in their own applications.

4.4 Results

4.4.1 Acoustic detections

The deployment period lasted 53 months, from 6 June 2007 to 15 April 2012, with a six-month data gap at the beginning of 2010 due to delayed maintenance of the mooring. In total, there were 321 5-day samples (spanning 1605 days) of sperm whale acoustic occurrence. The variability of sperm whale presence detected at OSP over the course of the five years (adjusted for seasonality, trend, and noise) is illustrated in Figure 4.4. A number of strongly anomalous detection events (red dots in Figure 4.4) punctuated the interannual variability of whale occurrence during this period. Unusually high numbers of acoustic detections were recorded in December 2007, October and December 2009, August 2010, January and March 2011, while sperm whale detections were anomalously low in November-December 2008, January and

March 2009, April, July and December 2011, and January 2012 (Figure 4.4). Strongly anomalous events are formally addressed on the next section.

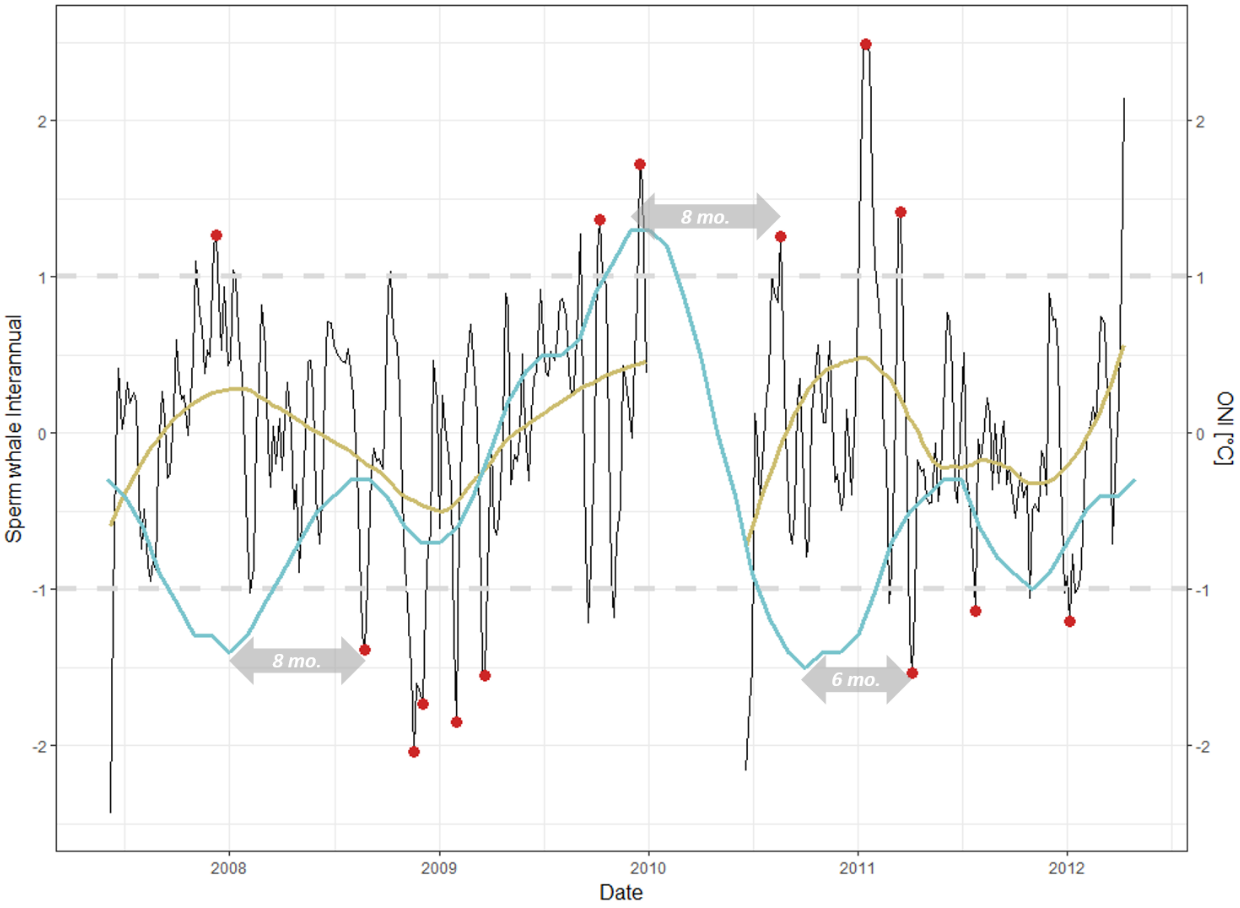

Figure 4.4 - Time series of sperm whale acoustic detections at Ocean Station PAPA (OSP), adjusted for seasonality, trend, and noise (i.e., the 'anomaly time series'; black line). The left y-axis represents sperm whale detections in five-day bins during the period June 2007 - April 2012. There was a data gap from 1 January to 15 June 2010 due to delayed maintenance of the mooring. A loess fit to the sperm whale modeled time series (brown curve) represents the smoothed low-frequency interannual variability of sperm whale occurrence at OSP that assisted with the qualitative interpretation in relation to climate indices. The blue curve represents the Oceanic Niño Index (ONI) values (right y-axis). Horizontal dashed gray lines highlight the thresholds that define

the strongly anomalous detection events (red dots) for the sperm whale occurrence as well as moderate El Niño–Southern Oscillation (ENSO) events. The gray arrows indicate the temporal lag between the strongest peak of an ENSO event and the first strongly anomalous detection event in sperm whale occurrence.

4.4.2 Data pre-treatment

Data gaps in certain oceanographic variables, as well as accounting for temporal lags, decreased the final sample size of the data set used for modeling to 125 samples.

Both the response and the oceanographic variables presented a strong, well-defined seasonal signal that dominated each annual cycle (Supplement,

Figure 4.5; see companion paper, Diogou et al. submitted). Specifically, near-surface temperature measurements, heat content, and strength of the shallow stratification integrated in the top 75 m showed similar seasonal patterns, with summer intensification and a steep drop during winter. Depth and strength of the permanent pycnocline, EKE, and current components showed low-frequency variability through time and considerable interannual variation. Chlorophyll-*a* concentration and Ekman upwelling showed much less seasonality or interannual variability. After all variables were de-seasonalized and de-trended (see Figure 4.3 for our signal decomposition approach), we made sure all variables met the stationarity assumption of time series analysis (Chatfield, 2004). The interannual signal captured was punctuated by several strongly anomalous events (Figure 4.4). Values that exceeded the deviation threshold [-1, 1], were evaluated as a strongly anomalous detection events.

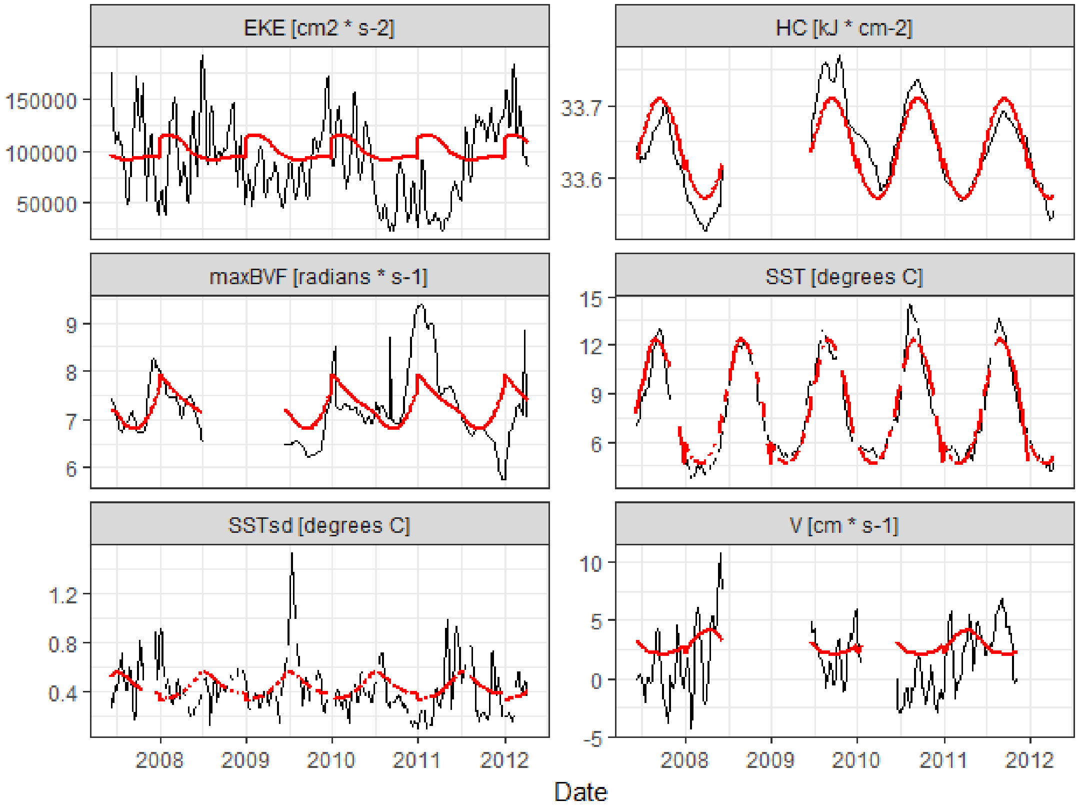

Figure 4.5 - Five-day binned time series of the important *in situ* and remotely sensed oceanographic variables (black line) that explain the interannual variability of sperm whale occurrence in the Ocean Station PAPA (OSP) study area. These variables appear in the FULL model. Removal of the periodic oscillations (red line) in all the variables resulted in the seasonally adjusted (i.e., deseasonalized) time series. Abbreviations are defined in Table 4.1.

4.4.3 Climatic context

During our sampling period, three moderate El Niño-Southern Oscillation (ENSO) events (2007-2008, 2009-2010, 2010-2011, see Figure 4.4) occurred. Starting in mid-2007, the Pacific was dominated by a moderate La Niña. By mid-2009, the tropical Pacific switched to a moderate El Niño that lasted until early 2010. By summer 2010 and until the end of our sampling period, the tropical Pacific exhibited a stronger and longer-lasting La Niña (Figure 4.4). Starting in 2007, the PDO was in positive phase until about August 2007 when it reverted to a negative phase (Supplement, Figure 4.9). In approximately August 2009, the PDO returned to warm anomalies. From May 2010 until the end of the sampling period, PDO remained in a negative phase.

4.4.4 Initial Modeling

The ACF and PACF plots revealed a strong autocorrelation between the global model's residuals. The correlation structure was identified as autoregressive with a moving average of 2, ARMA ($p = 2$, $q = 2$). This structure was included in the GLS global model.

The examination of the CCF plots indicated the existence of lagged relationships between the response variable and several of the oceanographic variables. CHL showed a lead of 10 lags (50 days), V of 4 lags (20 days), Zmax of 5 lags (25 days), maxBVF of 1 lag (five days), WUP of 6 lags (1 month), and S at 35 m of 8 lags (40 days), respectively. The remaining variables (intBVF75, EKE, U, D, SST, SSTsd, HC) either presented zero lag or no significant lags and therefore the zero-lag (i.e. the contemporaneous value) was used.

Based on VIF scores, D, U and maxBVF_1 were identified as collinear (Supplement, Table 4.4). Based on visual examination of bivariate scatter plots (Supplement, Figure 4.10), maxBVF_1 and SST showed the strongest linear correlation with sperm whale acoustic occurrence ($r = 0.29$, $p < 0.01$). Variables Zmax_5 and HC ($r = |0.18|$, $p = 0.02$), U and V_4 ($r = 0.22$ and $r = 0.17$, $p = 0.047$ and $p = 0.039$) also appeared to have some level of correlation.

Variables D ($r = 0.12$, $p = 0.21$) and S_8 ($r = 0.14$, $p = 0.09$) were only weakly correlated with sperm whale presence. There was essentially no correlation between CHL_{10} ($r = -0.022$, $p = 0.91$) or EKE ($r = -0.058$, $p = 0.67$) and sperm whale presence.

D and U ($r = -0.87$, $p < 0.01$), $maxBVF_1$ and $Zmax_5$ ($r = -0.68$, $p < 0.01$), EKE and S_8 ($r = 0.38$, $p < 0.01$), were identified as correlated pairs (Supplement, Figure 4.10). To reduce multicollinearity ($VIF > 4$), $Zmax_5$ and D were omitted from the global model for both the FULL and the IS models. S_8 was also removed from the global model for the FULL data set to reduce the VIF scores. Multicollinearity was not identified in the RS data set, and therefore no variable was removed for this analysis.

4.4.5 Model Selection

Details for the best multivariate GLSs for all three model categories (FULL, IS, RS) are provided in Table 4.3. The partial fits for each category of model are shown in Figure 4.6.

FULL model

The best candidate for the FULL model that included both *in situ* and remotely sensed variables explained 51% of the variance (adjusted $R^2 = 0.51$). It contained an intercept and had six explanatory variables as best descriptors of the interannual variability of sperm whale acoustic occurrence. The variables that explained this variability, in decreasing order of importance, were HC, V component at 35 m lagged by 4 steps (20 days), EKE, maxBVF lagged by 1 step (5 days), SST, and SSTsd (Table 4.2).

The modeling results (Table 4.3) showed a significant ($p < 0.05$) positive relationship between sperm whale acoustic occurrences and HC, maxBVF at a 5-day lag, SSTsd, and EKE. SST had lower evidence of significance ($p = 0.20$). Sperm whale acoustic detections increased with increasing values of these predictors. A significant negative relationship was observed between the sperm whale acoustic occurrence and V ($p = 0.01$, Table 4.3) with a 20-day lag, for which whale detections were high at low V values but decreased as these variable's values increased (Figure 4.6).

IS model

The IS model (Table 4.3) with the lowest AICc score included five explanatory variables that accounted for 46% of the interannual variability in sperm whale occurrence (adjusted $R^2 = 0.46$). According to this model, in order of importance, HC, $maxBVF_1$, and S_8 were significantly positively correlated with the sperm whale acoustic occurrence, while U and V_4 were negatively correlated with the response. U more strongly affected the relationship than V_4 and had the second highest importance weight (Table 4.2). Plots of the partial fits (Figure 4.6) showed that the sperm whale acoustic occurrence was generally high at high values and low at low values of $maxBVF_1$, HC, and S_8. Conversely, as indicated also by the FULL model, sperm whale detections were high at low U, and V_4 values, but decreased as these variables' values increased (Figure 4.6).

RS model

The final RS model (Table 4.3) with the lowest AICc score included two explanatory variables, and accounted for 36% of the variance (adjusted $R^2 = 0.36$). This model suggested that the measurements of SST and SSTsd were sequentially the most important of the satellite-measured variables. They both had a positive relationship with interannual variability of sperm whale acoustic occurrence in our study area. The partial fit plots (Figure 4.6) indicated a linear increase in sperm whale acoustic occurrence with increasing SST and SSTsd, the indicator of thermal front presence.

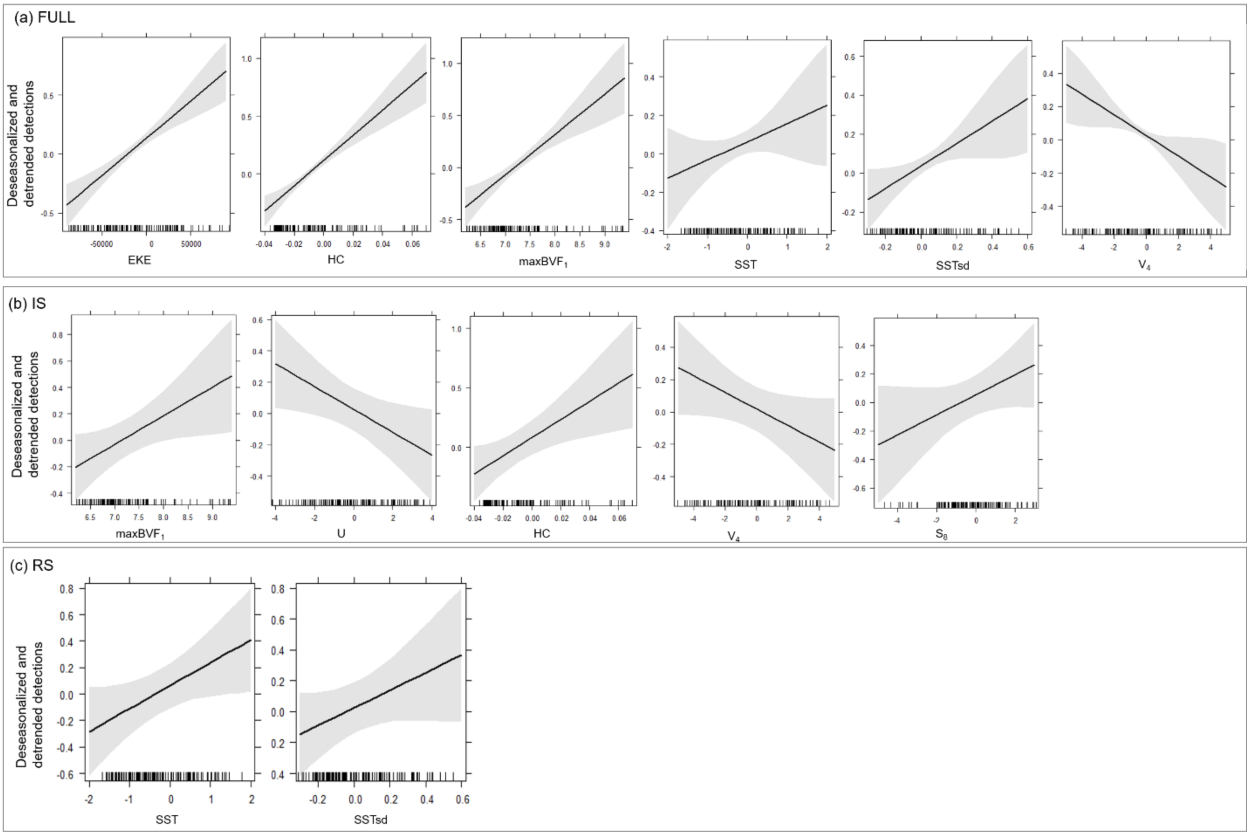

Figure 4.6 - Generalized least square (GLS) plots for variables with significant relationships with sperm whale deseasonalized and detrended acoustic detections . Plots are presented in three panels: (a) FULL model results that include both *in-situ* and remote sensed data, (b) *in situ* (IS) model results, and (c) remote sense (RS) model results. In each panel are presented the partial fits that display the effect of each explanatory variable (x-axis) on the response variable (y-axis), after accounting for the

effect of the other explanatory variables, with the 95% confidence intervals shaded. For all plots, the zero crossing has no direct interpretation since the data sets were deseasonalized and detrended. Abbreviations are defined in Table 4.1.

The models were deemed robust to regression model assumptions. There was no significant indication of heterogeneity in the residual plots for any of the models, and the Q-Q plots indicated normality with most of the points falling approximately along the reference line for the FULL (Supplement, Figure 4.11) and IS model. For the RC model, the distribution was slightly left-skewed but with small deviation from normality. ACF and PACF plots (Supplement, Figure 4.12), used to investigate the independency of residuals, showed little evidence for non-zero autocorrelations and indicated that temporal autocorrelation was adequately addressed.

FULL, IS, and RS comparison

The FULL model, with six explanatory variables, half remotely sensed and half *in situ* (HC, V_4, EKE, $maxBVF_1$, SST, and SSTsd), presented the lowest AIC and was selected over the IS and the RS models (Table 4.3). With AIC differences of 6 and 16.6, to the IS and RS models respectively, the FULL model performed significantly better. An AIC difference of greater than 10 (or 16.6 in the case of RS model) indicated that the RS model had essentially no support by the data and should be omitted from further consideration (Burnham and Anderson, 2002).

4.5 Discussion

This study provides insight into sperm whale acoustic occurrence in the GOA in relation to interannual environmental fluctuations. The FULL model (variance explained = 51%) showed that variables associated with ecosystem drivers from deeper in the water column (HC, $maxBVF_1$, V_4) appeared to be most important for a deep-diving species that feeds at the mesopelagic trophic level. Variables driving near-surface processes (SST, CHL), which are directly related to primary production, either appeared as less important in the FULL model, or had lower statistical significance. Important *in situ* variables in our study (HC, V_4, $maxBVF_1$, Table 4.3) have not been considered in previous studies of sperm whale occurrence patterns (Jaquet and Whitehead, 1996; Pirotta et al., 2011; Wong and Whitehead, 2014), limiting our ability to compare our models and results to published information.

The use of *in situ* oceanographic measurements of high temporal and spatial resolution proved efficient in characterizing the dynamic habitat preferences of sperm whales. Satellite data are often patchy due to cloud cover, especially in high latitudes, limiting the statistical power of habitat models. Here we were able to combine long-term *in situ* measurements of both oceanographic variables and sperm whale acoustic presence, increasing explanatory power in the final model. These results emphasize the importance of local-scale data when evaluating the relationship between cetaceans and their environment (Redfern et al., 2006; Pirotta et al., 2011). The combination of *in situ* measurements deeper in the water column with remotely sensed variables within a model provided the best results and increased explanatory power of the interannual variability of sperm whale occurrence in the offshore GOA. Both IS and RS models were thus considered less useful in the situation when both IS and RS variables are available.

4.5.1 Sperm whale predictors

HC was the most important variable in the FULL model and was positively correlated with sperm whale presence. Upper-ocean HC displays variability at interannual timescales (e.g. Tourre et al. 1999) and is commonly used as an indicator of climate change impacts on the marine environment (Levitus et al., 2012). In the study area, ecosystem responses to a HC decrease include a decline in presence of prey species like Pacific hake *Merluccius productus* and Humboldt squid *Dosidicus gigas* (Crawford et al., 2012). Conversely, increased ocean temperatures enhance growth of hatching squid (Rodhouse and Hatfield, 1990), and attract prey species such as thermophilic squid (Murata, 1988; Wing, 2005) that expand their geographic distribution northwards and perhaps offshore (Crawford and Mckinnell, 2013; Stewart et al., 2014), possibly attracting sperm whales to these areas.

Likewise, the interannual pattern in acoustic presence of sperm whales was secondarily related to an increase in SST, possibly reflecting periods of higher solar radiation and increased biological productivity at this high-latitude habitat. At lower latitudes and in the Mediterranean Sea, a negative relationship has been reported between sperm whale presence and seasonal SST (Jaquet, 1996; Rendell et al., 2004; Praca and Gannier, 2008a; Pirotta et al., 2011), likely because cooler water is an indication of stronger mixing/upwelling that supplies the upper layer with nutrients and increases primary productivity. However, in the North Pacific, marine mammal acoustic detections and abundance also increased at higher temperatures and seasonal SST (Keiper et al., 2005; Yen et al., 2005; Stafford et al., 2009). In the North Sea, sperm whale strandings were associated with positive temperature anomalies, linking sperm whale presence to prey movement (Pierce et al., 2007).

The interannual acoustic presence of sperm whales in the offshore GOA was positively related to the vertical stratification of the water column, specifically to a stronger and shallower permanent pycnocline, which likely leads to increased nutrient availability, ocean productivity, and prey aggregation in the study area. At OSP, a stronger permanent pycnocline may function as a barrier that prevents nutrients from the upper ocean from sinking to deeper layers of the water column via particle transport (Freeland et al., 1997; Wong et al., 1999). A shallower permanent pycnocline (which also leads to a shallow mixed layer), keeps phytoplankton and nutrients (particularly iron, a limiting factor at OSP) in a well-lit zone through winter and in a lower volume of water, increasing their concentration (Freeland et al., 1997) and enhancing primary and secondary productivity (Boyd et al., 1995). Additionally, with a shallower pycnocline, upwelling brings colder and nutrient-rich water to the surface. Likely for these reasons, sperm whale detections at OSP (this study) and marine mammal sightings off central California (Keiper et al., 2005) are strongly correlated with stronger stratification conditions.

Three variables associated with ocean circulation were important in the final FULL model (SSTsd, V_4, and EKE). The positive correlation between SSTsd and sperm whale acoustic presence suggests that that stronger thermal fronts provide favorable conditions for sperm whale prey. Fronts affect ocean productivity, aggregations of prey and top predators due to nutrient enhancement by mixing (Bakun, 1996; Palacios et al., 2006), and have been related to sperm whale aggregations in the North Pacific (Mizroch and Rice, 2013), North Atlantic (Hamazaki, 2002), and in the offshore Mediterranean

Sea (Gannier and Praca, 2007). Along the offshore region of Line P, 62% of the seabird species were also attracted to steep SST gradients and frontal systems (O'Hara et al., 2006).

Our results showed that periods with increased sperm whale presence corresponded with periods when currents showed stronger southward flows, warmer temperatures and increased eddy activity. At OSP, southward flows are generally associated with a relaxation of the Alaska Gyre (Bograd et al. 1999, Whitney & Freeland 1999) (Figure 4.1), whereas an intensified Alaska Gyre is known to cause a deepening of the mixed layer depth and colder winters in the Northeast Pacific (Deser et al., 1999; Mckinnell et al., 2012). A weakened Alaska Gyre allows for the intrusion of Haida and Sitka eddies, moving southwestward and westward from the coast, into the offshore GOA basin (Tabata and Tabata, 1982; Harrison et al., 1999; Crawford, 2002; Whitney and Robert, 2002) (Figure 4.1). These eddies transport iron-rich coastal water (Crawford et al., 2005) and organisms to the OSP region (Freeland, 2002; Mackas and Galbraith, 2002; Whitney, Crawford, and Yoshimura, 2005), likely concentrating prey and increasing foraging opportunities for predators such as sperm whales. Supporting this argument, EKE was of high importance in the FULL model. Eddies are prominent oceanographic features in the North Pacific and have been associated with marine apex predators (Palacios et al. 2006). In the North Atlantic, Wong & Whitehead (2014) also found a positive relationship between sperm whale acoustic occurrences and remotely sensed EKE. In the North Pacific, foraging patterns of fur seals (*Callorhinus ursinus*) were also positively related to EKE fields (Ream et al., 2005).

4.5.2 Sperm whale strongly anomalous detection events in relation to regional climate indices

The anomalously low sperm whale presence observed in August 2008 and January 2012 (Figure 4.4) coincided with periods with a deeper permanent pycnocline (Figure 4.2) and with particularly low records of squid catches in the central GOA (Ormseth and Spital, 2012). Conversely, one of the highest squid catches in 2007-2012 was reported for 2011 (Ormseth, 2012), when we recorded the highest number of sperm whale detections and the shallowest permanent pycnocline (Figure 4.2). In the South Pacific, Jaquet & Whitehead (1996) observed a similar relationship between sperm whales and high secondary productivity, emphasizing the trophic linkage.

The state of the ENSO cycle influences primary productivity at lower latitudes in the North Pacific (Corno et al., 2007) and affects ocean heat content, stratification structure, and circulation in high-latitude ecosystems (Whitney et al., 1998; Whitney and Freeland, 1999; Crawford et al., 2012), likely contributing to the variability of sperm whale acoustic presence as a result of shifting prey aggregations. At OSP, conditions we found related to higher sperm whale occurrence, such as higher temperatures, a shallower mixed layer and stronger stratification, a weaker Alaska Gyre, and enhanced eddy formation, are associated with El Niño (Jackson et al., 2006; Crawford et al., 2012). Haida eddies are larger during strong El Niño events (Crawford and Cummins, 2007), and both the Subarctic Frontal Zone and Transition Zone tend to shift further northwards (Nakamura, 2003), shifting squid and sperm whale distributions near OSP (Kubodera et al., 1983; Wing, 2005; Mizroch and Rice, 2013; Ramos et al., 2017). The opposite conditions occur during La Niña (Yasuda et al., 1997; Miller et al., 1998; Melsom et al., 1999; Deser et al., 1999;

Xie et al., 2000). The strongly anomalous events observed in sperm whale acoustic occurrences (red dots in Figure 4.4) could be related to ENSO events, as indexed by the ONI (blue line in Figure 4.4), after accounting for about an eight-month lag (grey arrows in Figure 4.4) for the mixed layer depth to respond to the thermal forcing and Ekman pumping altered by the ENSO component (Cummins et al., 2002; Li et al., 2005). Specifically, two La Niña peaks in January 2008 and October 2010 matched anomalously low sperm whale detections with lags of eight and six-months, respectively (grey arrows in Figure 4.4). During those periods, westerly winds (which strengthen the Alaska Gyre) decreased the ocean temperature in the NE Pacific (Crawford and Peterson, 2008), and Sitka and Haida eddies were much weaker than normal (Crawford and Mckinnell, 2009). The highest El Niño peak in December 2009 (blue line in Figure 4.4) carried warm water northwards (Crawford and Robert, 2011), and matched peaks in sperm whale occurrence, about eight and 12 months later (August 2010 and January 2011). Originating in the equatorial Pacific, an ENSO event typically takes a few months to reach the Northeast Pacific region (Mckinnell and Crawford, 2007), while the arrival of Humboldt squid (a critical component of the sperm whale diet in other parts of the Pacific; Clarke & Paliza 2001, Jaquet & Gendron 2002, Davis et al. 2007, Stewart et al. 2014) and sperm whales in Alaska may take about four months following this environmental change (Mizroch & Rice 2013, Ramos et al. 2017, Wing 2005). This difference in timing may explain the observed temporal lag between the ENSO peak in the tropics and the peak in acoustic sperm whale occurrence in the study area.

The PDO cycle can also play a role in the oceanographic conditions, and possibly the presence of sperm whales, at OSP. A weakening of the Alaska Gyre, a shoaling of the permanent pycnocline, an increased temperature and

HC occur during warm PDO phases, while the opposite conditions prevail during cold PDO phases (Cummins et al. 2002, Crawford et al. 2012, Mantua et al. 1997). From 2007 to 2012, the low and the high anomalies of sperm whale occurrence appeared to correspond to the negative (cold) and positive (warm) phases of the PDO, respectively (Supplement, Figure 4.9). Stewart et al. (2014) suggested that the PDO, which was related to squid abundance, affects midwater oxygen through pycnocline movements. A deepening of the pycnocline leads to an increase in the temperature in the deeper water column, which may cause unfavorable conditions for spawning squid (Zeidberg et al., 2011). Conversely, a shoaling of the permanent pycnocline could facilitate sperm whale foraging efficiency, as prey would be driven to shallower water. However, the PDO operates at a much lower frequency than ENSO, and five years of sampling at OSP are not sufficient to adequately identify relationships between the PDO and ecosystem variables.

4.5.3 Climate variability driving sperm whale occurrence – proposed mechanism and summary

For the North Pacific, climate models predict a contraction of the Alaska Gyre and a northward migration of the Transition Zone of up to 1000 km by 2100 (Hazen et al., 2012). A consequent intrusion of eddies and enhancement of currents and fronts in the OSP region would support concentrations of prey and attract mesopelagic fauna and top predators (Frederiksen et al., 2006; Mackas et al., 2007; Hatun et al., 2009). Additionally, near OSP, a warming of surface waters and a shoaling trend of the permanent pycnocline has been detected over the past four decades (Freeland et al., 1997). Thus, our results are consistent with the idea that an increase in SST/ocean heat content and stratification in the northeastern subarctic Pacific would increase ocean productivity in the region by gradual nutrient enrichment (Polovina et al., 1995; Freeland et al., 1997; Whitney et al., 2013) and benefit sperm whales. In contrast, a deepening of the main pycnocline due to increasing temperature and the resulting reduction in nutrient supply and biodiversity was observed in subtropical zones (Polovina et al., 1995), the coastal California Current (Palacios et al. 2004), the coastal northern GOA (Lagerloef, 1995), and the tropics (Mayhew et al., 2008; Hazen et al., 2012). In the Galapagos, a strong negative correlation between sperm whale foraging success and ENSO conditions has been reported (Whitehead, 1996; Rendell et al., 2004), and emigration has been identified as the main strategy of sperm whales when facing a decline in prey resources (Whitehead, 1996). We speculate that sperm whales at low latitudes, facing decline of their prey, might move into regions with more favorable feeding conditions like the offshore subarctic. Whitehead et al. (2008) predicted an increase of deep diving marine mammals at high latitudes and a loss of biodiversity in the tropics by 2080 due to ocean warming. From the interpretation of our results, it appears that sperm whale occurrence in the offshore GOA may be increasing, possibly due to an increase in prey availability driven by El Niño events, the northward migration of the Transition Zone, and the contraction of the Alaska Gyre. Decadal-scale events (i.e., the PDO) may also play a role, but our time series was not sufficiently long to address this question.

Finally, with the best model explaining up to 51% of variability in sperm whale occurrence, there is still unexplained variance. Undeniably, the leap from physical forcing to the top of the food chain and the depths of the ocean is enormous. Additionally, this study was limited by a single station and one time series of whale data, which did not allow evaluations of the effect of larger spatiotemporal scales. Investigations of the relationship between sperm whales and their environment in a multiscale level could perhaps help explain part of the remaining 49% of variability. Investigations of the sperm whale spatial distribution with respect to the oceanographic explanatory variables (such as the depth of the permanent pycnocline, EKE, HC, etc.) would provide more insight to the whale habitat preferences. For instance, fine-scale tag data that record the whale's diving behavior, and large-scale deployments of acoustic recorders, in conjunction with in situ and remotely sensed measurements of environmental variables, would allow for a more integrated and holistic understanding of the whales' habitat preferences and ecology (Palacios et al., 2013). The applicability and validation of the model to other areas remain to be addressed in future studies. For the same reasons, the anomalous events of the sperm whale interannual variability do not all follow the relationship described above for the ENSO peaks. The whale data currently available are not sufficient to investigate complete oscillations of the large-scale climate variability. Continuation of the acoustic monitoring at OSP will allow for strategic assessment of climate-ecosystem responses even at intra/interdecadal time scales that are required for examinations of larger scale oceanographic regimes.

4.6 Conclusions

After six decades of research at Line P and continuous recording of ocean conditions in the northeastern subarctic Pacific, this is the first study to use these oceanographic measurements to explore the relationship with whale occurrence at OSP. With a model explaining up to 51% of variability in sperm whale occurrence, we were able to characterize the response by an endangered marine species to oceanographic processes in the inaccessible offshore GOA. Our modeling results indicate that ocean heating, stratification, and circulation dynamics at OSP are important drivers of ecosystem change, as reflected in the low-frequency variations of an apex predator's occurrence. The strongly anomalous events that punctuated the interannual variability of sperm whale occurrence at OSP were likely related to prey availability pulses, driven by oceanographic conditions defined by large-scale climatic features of the Pacific, such as ENSO. Our modeling approach provides a framework and a baseline to further address the potential ecological consequences of anthropogenic activities and global climate change on the oceans. For instance, a long-term increase in water temperature may lead to a potential increase in sperm whale presence in the GOA, which in turn may affect Alaskan fisheries. More specifically, the interaction between depredating sperm whales and sablefish fishing operations in Alaskan waters (Thode et al., 2007; Straley et al., 2014) may be exacerbated if whale abundance increases in the GOA, increasing the availability of animals in the area to potentially engage in depredation activity.

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4.8 Tables

Table 4.1 - Response and explanatory variables used for the time series analysis, with their corresponding abbreviations. In the last column, the number next to the abbreviated name as a subscript indicates the temporal lag chosen for the analysis. The absence of a number indicates that the zero-lag measurement was used.

Type	Measured	Description	Abbreviation /symbol	Highest significant lag
Response		Number of days in 5-day window with sperm whale acoustic detections	Detection	
Explanatory	***In-situ***	Zonal current velocity at 35m (*positive for west-to-east motion*)	U	U
		Meridional current velocity at 35m (*positive for south-to-north motion*)	V	V_4
		Current speed at 35m	S	S_8
		Current direction at 35m	D	D
		Integrated heat content (0-300m)	HC	HC
		Integrated Brunt–Väisälä frequency for shallow pycnocline (0-75m)	intBVF75	intBVF75
		Maximum Brunt–Väisälä frequency for permanent pycnocline (81-200m)	maxBVF	$maxBVF_1$
		Depth of maximum Brunt–Väisälä frequency for permanent pycnocline (81-200m)	Zmax	$Zmax_5$
	Remotely sensed	Eddy kinetic energy	EKE	EKE
		Ekman upwelling	WUP	WUP_6
		Sea surface temperature	SST	SST

	Standard deviation of the sea surface temperature	SSTsd	SSTsd
	Chlorophyll-*a* concentration	CHL	CHL$_{10}$

Table 4.2 - The importance of individual variables from the multivariate GLS model selection process. The variables in bold are the ones that emerged as important predictors from the univariate models. Abbreviations are defined in Table 4.1.

Model category	Variable	Importance
FULL	**HC**	0.89
	V_4	0.87
	EKE	0.82
	$maxBVF_1$	0.81
	SST	0.68
	SSTsd	0.59
	U	0.56
	intBVF75	0.45
	CHL_{10}	0.35
	WUP_6	0.21
IS	**HC**	**0.86**
	U	**0.83**
	V_4	**0.7**
	$maxBVF_1$	**0.6**
	S_8	**0.46**
	intBVF75	0.31
RS	**SST**	**0.64**
	SSTsd	**0.5**
	CHL_{10}	0.34
	WUP_6	0.24

	EKE	0.24

Table 4.3 - Final multivariate GLS models for the acoustic detections of sperm whales in the OSP study area. Included is each important explanatory variable (abbreviations are defined in Table 4.1) along with the coefficient value (coef). The asterisks represent the *p*-values, as follows: $p > 0.05^{ns}$ (ns: not significant), $p \leq 0.05^{*}$, $p \leq 0.01^{**}$, $p \leq 0.001^{***}$, $p \leq 0.0001^{****}$. The total and the residual degrees of freedom (Tdf, Rdf), the amount of variance explained (adjusted R^2), and the Akaike Information Criterion for small samples (AICc) are reported for each model. The details of all three categories (Cat.; full, IS, RS) of models are presented. See Table 4.1 for variable abbreviations.

Cat.	**Variable**	**Coefficient**	**SE**	**Tdf**	**RDf**	**R^2**	**AICc**
Full	HC	10.899****	1.807	125	118	0.51	196.5
	$maxBVF_1$	0.388****	0.083				
	EKE	6 x 10-5****	0.000				
	V_4	-0.062**	0.024				
	SSTsd	0.573**	0.240				
	SST	0.095^{ns}	0.073				
IS	HC	7.593**	2.828	125	119	0.46	202.5
	$maxBVF_1$	0.216*	0.097				
	U	-0.073*	0.032				
	V_4	-0.051^{ns}	0.027				
	S_8	0.070^{ns}	0.031				
RS	SST	0.173*	0.082	125	122	0.36	213.1
	SSTsd	0.572^{ns}	0.346				

4.9 Supplementary Data

Table 4.4 - Variance inflation factors (VIF) for the three data set categories. Values include the VIF scores before and after we accounted for multicollinearity by removing certain variables. See Table 4.1 for variable abbreviations.

t Cat.		**CHL_{10}**	**$Zmax_5$**	**intBVF75**	**$maxBVF_1$**	**EKE**	**D**	**S_8**	**U**	**V_4**	**SST**	**SSTsd**	**HC**
	All variables	1.55	2.79	3.15	**5.80**	2.25	**6.45**	1.31	**6.93**	1.95	2.43	1.33	1.68
	Removed collinear	1.26		2.54	3.81	2.19			1.44	1.67	2.11	1.22	1.49
	All variables		2.59	1.82	3.74		**4.60**	1.12	**5.26**	1.34			1.34
	Removed collinear			1.54	1.92			1.11	1.18	1.25			1.21
e	*All variables*	1.10				1.05					1.09	1.07	

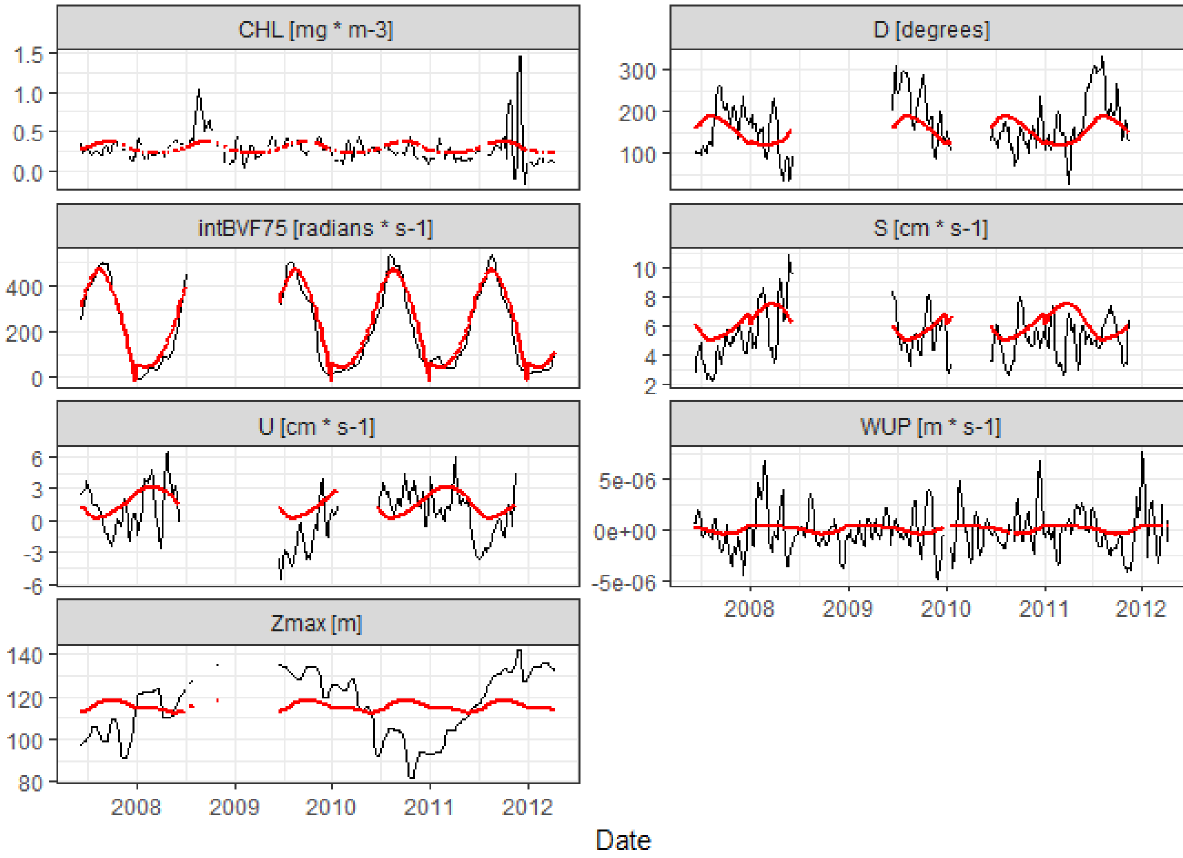


Figure 4.7 - Five-day binned time series of the explanatory variables (black line) that were considered in the initial models but were not included in the best model. Removal of the periodic oscillations (red line) in all variables resulted in the seasonally adjusted (i.e., deseasonalized) time series. See Table 4.1 for variable abbreviations.

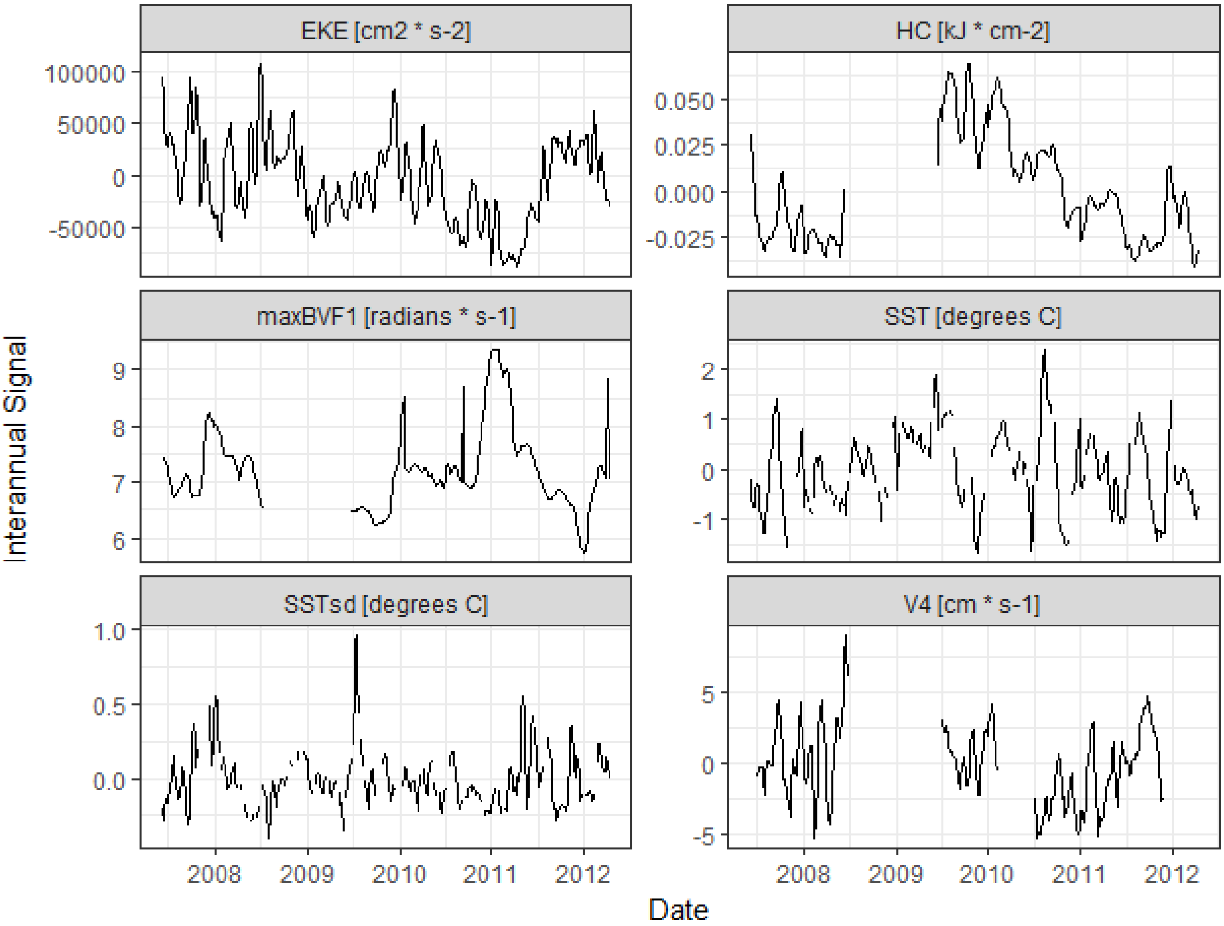


Figure 4.8 - Five-day binned time series of the interannual signal (i.e. the 'anomaly time series') of all important predictors for the sperm whale occurrence in the Ocean Station PAPA (OSP) study area. See Table 4.1 for variable abbreviations.

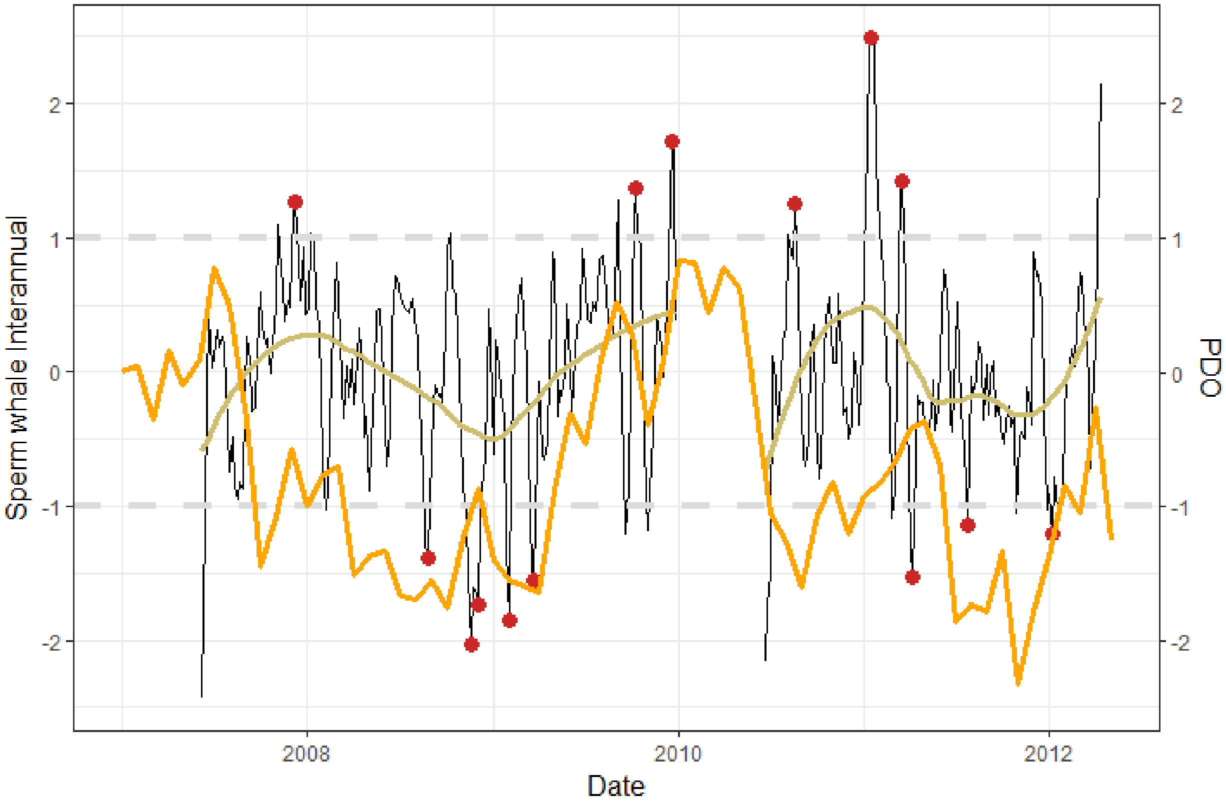
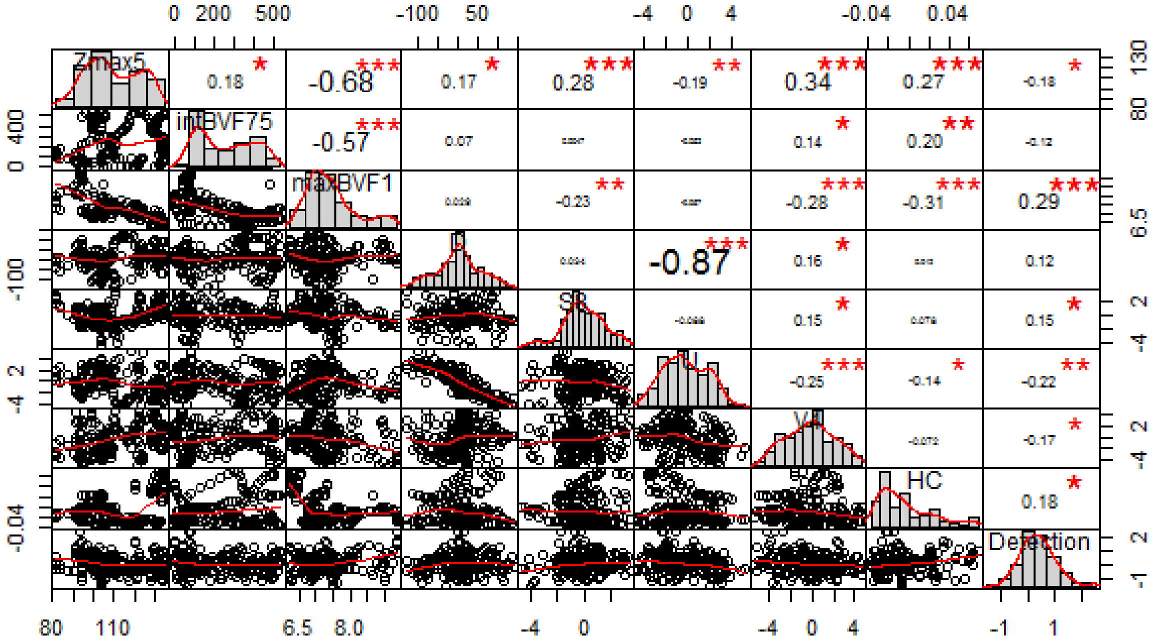


Figure 4.9 - Time series of sperm whale acoustic detections at Ocean Station PAPA (OSP), adjusted for seasonality, trend, and noise (i.e., the 'anomaly time series'; black line). The left y-axis represents sperm whale detections in five-day bins during the period June 2007 - April 2012. There was a data gap from 1 January to 15 June 2010 due to delayed maintenance of the mooring. A loess fit to the sperm whale modeled time series represents a smoothed low-frequency interannual variability (yellow curve) of the sperm whale occurrence at OSP that is used for interpretation in relation to climate indices. The orange curve represents the Pacific Decadal Oscillation (PDO) values (right y-axis). Horizontal dashed gray lines highlight the thresholds that define the strongly anomalous detection events (red dots) for the sperm whale occurrence.


Zmax5
intBVF75
maxBVF1
D
SR
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V
HC
Detection
0.18 *
-0.68 ***
0.17 *
0.28 ***
-0.19 **
0.34 ***
0.27 ***
-0.18 *
-0.57 ***
0.07
0.14 *
0.20 **
-0.12
-0.23 **
-0.28 ***
-0.31 ***
0.29 ***
-0.87 ***
0.16 *
0.12
0.15 *
0.15 *
-0.25 ***
-0.14 *
-0.22 **
-0.17 *
0.18 *
0 200 500
-100 50
-4 0 4
-0.04 0.04
80 110
6.5 8.0
-4 0
-4 0 4
-1 1
0 400
-100
2 -4
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130 80
6.5
2 -4
2 -4
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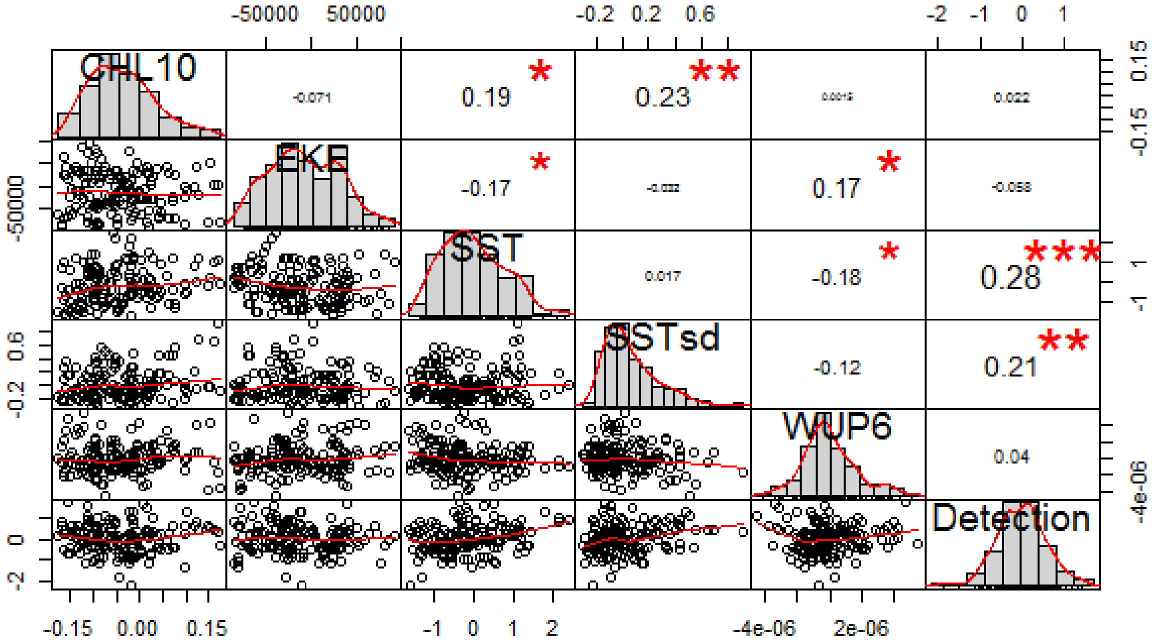
CHL10
EKE
SST
SSTsd
WUP6
Detection
-0.071
0.19 *
0.23 **
0.0015
0.022
-0.17 *
-0.032
0.17 *
-0.058
0.017
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-50000 50000
-0.2 0.2 0.6
-2 -1 0 1
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-1 0 1 2
-4e-06 2e-06
-50000
0.6 -0.2
0 -2
0.15 -0.15
1 -1
-4e-06

Figure 4.10 - Scatterplot matrices with histograms illustrating the bivariate relationships among the (a) *in-situ* and (b) remotely sensed variables and the sperm whale acoustic occurrence. The absolute correlations with significance asterisks (0.05*, 0.01, 0.001***) between variables are shown in the upper triangle. The diagonal depicts the univariate distribution of all variables with kernel density overlays. See Table 4.1 for variable abbreviations.**

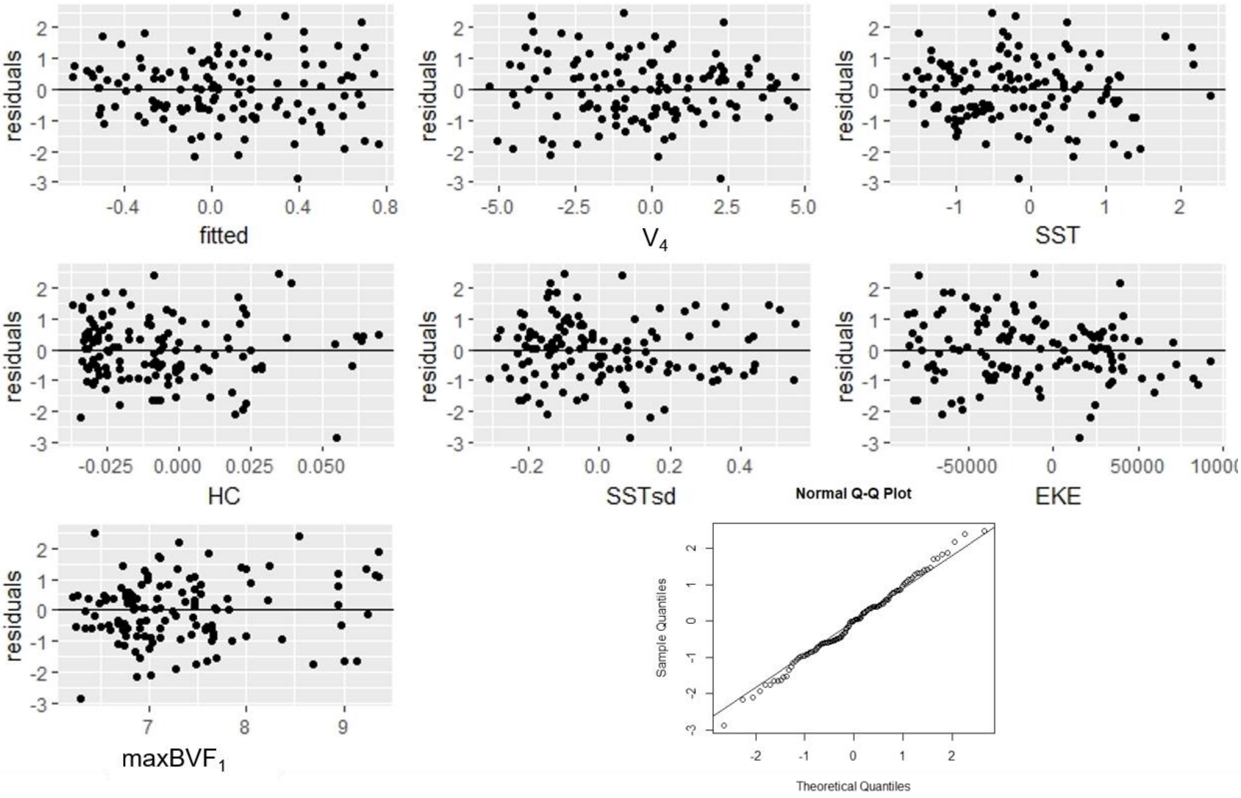

Figure 4.11 - Diagnostic plots for the variables with significant relationships with interannual sperm whale acoustic occurrence. FULL model results that include both *in-situ* and remote sensed variables are presented. Two types of plots are shown: (1) residual plots and (2) diagnostic quantile-quantile (Q-Q) plots to evaluate how well the model fits the data and if it complies with the model assumptions. There were no significant indications of heterogeneity in the residual plots for any of the models. See Table 4.1 for variable abbreviations.

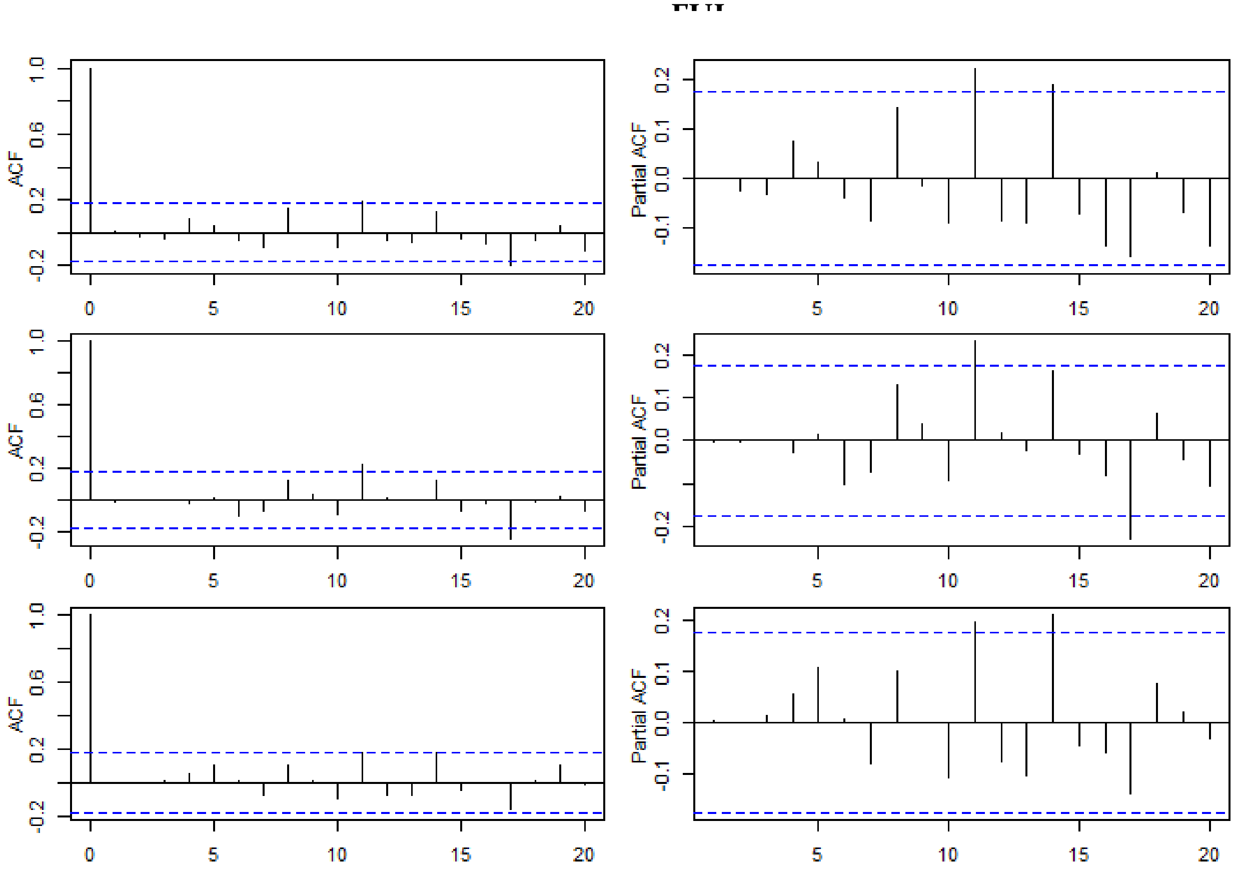

Figure 4.12 - Autocorrelation (ACF) and partial autocorrelation (partial ACF) plots for the residuals of the FULL model for the first 23 lags. Each lag corresponds to 5 days. These correlograms show that the autocorrelations for first and the 17th lag in the ACF exceed the significance bounds in the IS model, and both the 11th and the 14th from the partial ACF plots exceed the significance bounds in the FULL and RS models, and the 11th and 17th in the IS model.

5. Conclusions

The real voyage of discovery consists not in seeking new landscapes
but in having new eyes.

— Marcel Proust, A la recherché du tempts perdu

Imagine being in the vast open-ocean, trying to collect observations of whales that spend almost their entire time in the unseen depths, and only emerge on the surface for short 15 min breaks to catch their breath and socialize. You might feel like you are looking for a needle in a haystack. Now imagine the practically impossible task of doing this for the entire year, day and night. Conveniently, some species produce unique and loud sounds while diving in the oceans' darkness and scientists have developed underwater 'bugs' to eavesdrop on them. Sperm whales are exceptionally skilled at extreme deep diving, and particularly difficult to observe using visual methods, especially when we are interested in locations far from the shores and for the long-term. Luckily, sperm whales are notoriously vocal.

5.1 Insights into Sperm Whale Ecology

Using passive acoustics allowed me to demonstrate that sperm whales are present year-round at OSP, 900 km off the coast of the GOA in the North Pacific, and at Pylos, 10 km off the west Peloponnese coast in the east Mediterranean Sea, while they are absent from Athos, 30 km off the Athos Peninsula (Chapters 2 and 3). These studies highlight the importance of the first two habitats for sperm whales and represent the longest PAM research efforts for odontocetes in the offshore GOA and the Greek Seas to date. Additionally, this work provides the first solid year-round record of sperm whale occurrence at the Hellenic Trench (Chapter 2) and the first attempt to quantify and explain the sperm whale temporal patterns in the GOA (Chapters 3 and 4).

Previous sperm whale density estimates in the Ionian Sea are among the highest in the Mediterranean (Gannier et al., 2002; Boisseau et al., 2010) and their presence at Pylos during all months was anticipated. The almost continuous delphinid acoustic detections also indicate a rich cetacean abundance and diversity. However, it was not too long ago when the Greek Seas were considered marine deserts, with poor cetacean fauna due to their oligotrophy (Marchessaux, 1980). At the same time, the open ocean in the GOA is in the vicinity of the oligotrophic Pacific Subtropical Gyre and is a less productive ecosystem compared to the adjacent coast. The OSP region is characterized as a 'high-nitrate, low-chlorophyll', and there are reports from Yankee whalers indicating little whaling effort and limited catches (Mizroch and Rice, 2013). Additional reports of high sperm whale abundance in seemingly oligotrophic waters (Wong and Whitehead, 2014) emphasize on this apex predator's ability to occupy an ecological niche that is inaccessible to many other top predators. In addition, sperm whales specialize in prey items with limited commercial value. Rendell and Frantzis (2016) explain the paradox of an oligotrophic sea sustaining a large predator with the independence of deep-sea squid from the basis of the food chain on the surface; these two trophic levels, however, are difficult to completely separate. Sperm whale detections at OSP, in the GOA, were about seven times higher than at Pylos, in the Ionian Sea (71% and 13% of the recording days respectively; Chapters 2 and 3). An anticipated result that highlights the difference in scale between the Pacific and the Mediterranean ecosystems; there is an enormous gap in marine productivity levels, availability of resources, prey aggregations and abundance of apex predators between the two areas, with the Pacific indicatively sustaining the largest fishery in the world. It is likely that the reasons for this difference are the same ones acting on the difference in the maximum size between individuals that inhabit the Mediterranean Sea and the oceans.

The topographic characteristics of both sites fit the previously described habitat preferences for the species. At OSP, the oceanic habitat with nearby seamounts; and at Pylos, the continental shelf on the steep edges of the Hellenic Trench; both make suitable habitats for sperm whales. Even though the Athos location is also defined by a deep basin, trenches and troughs, certain oceanographic features that could attract sperm whales and their specialized prey may be lacking from the site. The most plausible explanation for the absence of sperm whales from what would appear a suitable habitat for the species, is that the location of Athos Station is likely part of the ecological niche of a different teuthophageous odontocete, the Risso dolphin (*Grampus griseus*). The Risso's dolphin also preys on bathypelagic cephalopods, therefore there is an overlap of the sperm whale and the Risso's diet (Milani et al., 2018). To avoid competition, in the Northwest Mediterranean, there is differentiation of the ecological niche of the two species, with Risso's dolphin showing a preference for the shallower upper part of the continental slope while the sperm whale is most frequently observed in further off-shore waters and a deeper part of the slope (Praca and Gannier, 2008b). In fact, at Athos, most of the delphinid acoustic detections were consistent with the acoustic characteristics of Risso's vocalizations. These detections (Chapter 2) provide some evidence that Athos (400 m water depth) in the North Aegean Trough, which is significantly shallower than Pylos (1680 m water depth) in the Hellenic Trench, is likely dominated by the presence of another deep-diver, the Risso's dolphin (mean depths of the predicted presence: 638 m for Risso's dolphin, 1746 m for the sperm whale; Praca, 2008). Theoretically, the spatial segregation of two cephalopod predators would help reduce competition for food resources.

Within the Pacific sperm whale population, this work assumes a geographical sexual segregation, suggesting that the detections at OSP belong to solitary males or male bachelor groups that use the site for foraging, while females remain in lower latitudes. This theory is supported by the absence of coda recordings at this site during the five-year sampling and previous work (Whitehead, 2003). On the other hand, social groups are likely included at the Pylos recordings, since usual clicks, creaks, and codas were detected. In Chapters 2 and 3, results demonstrated that there are more sperm whale detections during the warmer seasons both in the GOA and in the Greek Seas. This seasonal pattern is clearer and more prominent at the North Pacific site, where larger changes occur in the water column properties during different seasons. However, the data from the Greek Sea stations were not sufficient to determine accurately temporal patterns and a full seasonal cycle. Future work should focus on collecting a longer time series of acoustic recordings from the Greek Seas in order to better quantify temporal patterns of cetacean variability.

The sperm whale seems to be opportunistic and nomadic in its feeding and moving strategy, exploiting habitats of steep slopes, and offshore pelagic waters with prevalent frontal systems and eddies (Wong et al., 1999; Gannier et al., 2002; Gannier and Praca, 2007; Pirotta et al., 2011; Mizroch and Rice, 2013). Particularly in the open ocean, oceanographic features are expected to play perhaps a more important role in sperm whale habitat use than topography, creating *oases* within the ocean *deserts* (Godø et al., 2012). Results in Chapter 4 demonstrate that the interannual presence of sperm whales in the offshore GOA increases with a warmer, more stratified water column, with a stronger southward flow and increased eddy activity. Even though I did not quantify the relationship of sperm whale presence and oceanography in the

Greek Seas, previous work has demonstrated a positive relationship between sperm whale occurrence and lower water temperatures (decreased SST) (Praca and Gannier, 2008a; Pirotta et al., 2011). An interpretation of this disagreement is likely based on the difference in limiting factors for ocean productivity based on geographic variation. Growth will be as great as allowed by the least available resource. In higher latitudes, like the OSP region, the surface water is cold, and strong winds cause the water column to mix and transport nutrients to the euphotic zone; here, ocean productivity is often limited by sunlight whose intensity is reflected on SST levels. In lower latitudes and warmer seas like the Mediterranean, where sunlight is abundant and intense, ocean productivity is dictated by nutrients supplied through water mixing, localized upwelling events and increased turbulence that cause lower SSTs.

This work, importantly, provides insight into the potential effects of global warming on the sperm whale population in the Pacific Ocean. Results from time-series modeling (Chapter 4) highlight the importance of including in-situ oceanographic measurements in a habitat model, and showed that increased ocean heating, stratification and circulation favor the sperm whale presence in the offshore GOA from year to year. These conditions, as expressions of the relaxation of the Alaska Gyre and the intrusion of coastal mesoscale eddies at OSP, also appear to be associated with stronger El Niño events and warm phases of the PDO. Northward migrations of the Subarctic Frontal Zone and North Pacific Transition Zone occur during El Niños, with those large frontal areas transferring and aggregating prey close to the OSP. The North Pacific Transition Zone also oscillates longitudinally with season, and this work supports the possibility that the Transition Zone plays a crucial role in the seasonality observed in sperm whale acoustic occurrence in the GOA (Chapter

3). Although we do not have definitive evidence yet, the available data hint that while the Pacific Ocean is warming, intensification of El Niño events may lead sperm whales to higher latitudes where more food is available compared to the Tropics. Longer time series that extend to inter-decadal scales and more acoustic stations in lower latitudes are required to verify those speculations. Equally long-term recordings are needed from the Greek Seas to examine temporal patterns and climate-change related questions.

The water column stratification appears to be an important environmental feature for the distribution of prey and sperm whales in the North Pacific (Chapters 3 and 4). In our results, both the year-round and the interannual sperm whale presence at OSP are associated with the strength and the depth of the permanent pycnocline. Sperm whales are perfectly adapted in the marine environment and are extremely successful predators. Having developed a highly sophisticated acoustic organ, they can locate prey and other structures within the water column about tens of km away (Chapters 2 and 3). At the same time, changes in water temperature, salinity and overall density make a different acoustic footprint, since sound propagation critically depends upon these features. If the permanent pycnocline, which essentially is a dense layer of water at about 100 m depth, is an important indication of prey, then can sperm whales use their clicks to identify the pycnocline and use that information to assess vital information for their survival? Would sperm whales be able to detect it and evaluate the depth and strength of the pycnocline, if it translates to food aggregations? It is likely that sperm whales use their echolocation system for crucial environmental conditions, but if focused research is not implemented, this will remain in the sphere of speculation.

Beyond the ecological merit of this work, the statistical method applied at the habitat-modeling analysis (Chapter 4) introduced the value of seasonal decomposition at the data set, the benefit of isolating the temporal signal of interest, and the use of temporal lags between the response and the explanatory variables. With the final model explaining up to 51% of variability in sperm whale occurrence in the GOA, this work exceeded the usual amount of variance explained in cetacean-habitat modeling analyses (Redfern et al., 2006). Nevertheless, my findings offer a reminder that our understanding of sperm whale habitat preferences is incomplete, since the leap from physical forcing to the top of the food chain and the great depths of the ocean is enormous. However, information on the sperm whale occurrence patterns can provide substantial understanding of their prey (Clarke, 1980). Considering the gap in our knowledge about the meso- and bathy- pelagic cephalopod communities (escape trawls and nets and are difficult to study with echosounders; Starr and Thorne, 1987) the results of this study could also assist predictions of deep-sea squid abundance and distribution for potential fishery development in the GOA (Ormseth, 2013). Lastly, a valuable methodological contribution of this work has been the use of *in-situ* measurements that allowed examination of the oceanographic conditions deeper in the water column, which is the basis of higher trophic levels. Even though satellite evaluations of primary productivity are useful for the sea surface conditions, they can only function complimentary to the understanding of a top predator's ecology.

5.2 The Silent World No More

Wide use of hydrophones has revealed a not-so-silent underwater world (Haver et al., 2017). The world ocean is in fact a noisy place, and Cousteau and

Dumas' (1953) book title has proved to be a misnomer. The underwater soundscape is comprised of a variety of sounds of natural and anthropogenic sources that dominate different frequency bands (Wenz, 1962). The low frequency band (10 to 500 Hz) corresponds largely to noise produced by human activities, including commercial shipping and seismic exploration, and due to little attenuation, propagates for long distances. The medium frequency band (500 Hz to 25 kHz) includes mostly ambient sound that results from natural sources such as wave action, ocean spray and rainfall, and propagates a few tens of km. Anthropogenic sources such as sonars and small-size vessels also contribute to the mid-frequency band. The high frequency band (>25 kHz) corresponds largely to thermal noise and attenuates the fastest (Hildebrand, 2009). Even though marine wildlife that depends on sound for vital functions, has adapted to natural sounds, it is increasingly concerning how that wildlife is affected by manmade noise. These effects range from behavioral responses to acoustic trauma to fatalities and their severity depends on the characteristics of both the noise and the species. For instance, the frequency, amplitude, duration, distance from the noise source, and the behavioral state, age, gender and health of the whale, can change the impact induced (Weilgart, 2007a). However, assessments of these effects, particularly in a population level, are particularly difficult. With the ambient noise levels in the low frequencies (where shipping occurs) having increased by about 11 dB in the North Pacific within the last few decades (Andrew et al., 2002), and with a 23% increase in transit activity in the Mediterranean Sea within the last 10 years, measurement of baseline ambient sound levels are considered crucial for monitoring and conservation efforts.

Results from this work highlight the important contribution of low-frequency (below 1 kHz) noise to the soundscape of the Ionian Sea. Ambient sound levels, largely generated by ship traffic, were the highest at Pylos, in comparison to OSP and Athos (Chapters 2 and 3). At Pylos, the low frequencies are louder (64 dB re 1 $\mu Pa^2/Hz$, <1 kHz), by 4-5 dB than OSP (60 dB re 1 $\mu Pa^2/Hz$, <1 kHz) and Athos (59 dB re 1 $\mu Pa^2/Hz$, <1 kHz). This difference is a result of the frequent cargo ship, tanker and ferry passages (Richardson and Würsig, 1995) at the vicinity of Pylos, reflecting the large-vessel traffic shown in Figure 5.1. The mid-frequency sounds, that include the frequency that sperm whale clicks are omnidirectional (3 kHz), are of the lowest amplitude at Athos (Athos: 50, Pylos: 55 dB, OSP: 55 re 1 $\mu Pa^2 Hz^{-1}$) but data from this area were insufficient to make safe comparisons. However, natural sound sources like storms (waves, strong winds and rainfall) are included in the mid-frequency band, and are prevalent in the areas of OSP and the Greek Seas, particularly in winter. Thus, ambient noise levels increase with increasing wind speed in the frequency range in which we detected sperm whale clicks (Wenz, 1962; Chapter 2). Overall, there are indications that sperm whales at Pylos are exposed to higher ambient sound levels than the sperm whales at Athos or OSP at lower frequencies (<1 kHz). Large-vessel traffic increases globally and is the greatest anthropogenic contributor to ocean noise in the low-frequency band. Even though large-vessel noise is not in the same frequency band as sperm whale clicks, the elevated low-frequency noise indicates increased shipping traffic, which poses additional risks for sperm whales in the form of ship strikes.

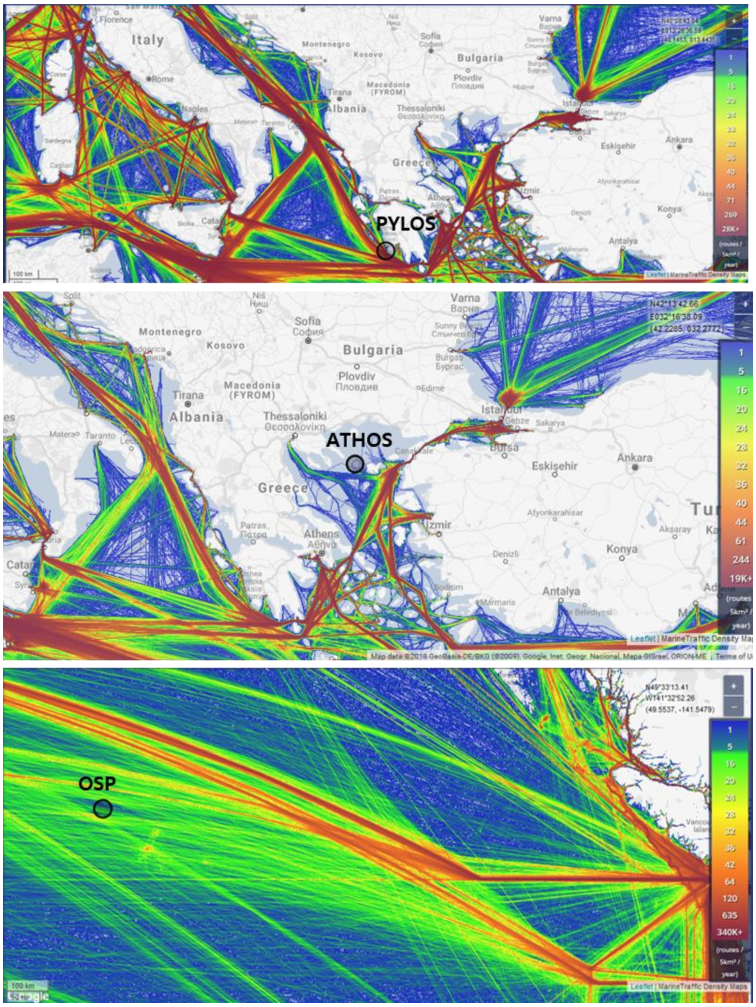

Figure 5.1 - Density maps of the main shipping lanes of large boats (GT 25K - 60K, top map), very large boats (GT > 60K, middle map) in the Greek Seas, and all traffic in the Gulf of Alaska. The locations of Pylos, Athos, and OSP are represented by the black circle of a 20 km radius at the top, middle and bottom panels, respectively. All shipping traffic density maps were extracted from www.marinetraffic.com.

In summary, this work shows an important overlap between higher underwater noise levels and cetacean acoustic activity and diversity at the Pylos site. A *hotspot* for sperm whales in the Greek Seas occurred in an area with a strong ‘human footprint’, which helps identify the focus of regional marine management and conservation efforts.

5.3 My acoustic *PAL*

I first set out on this study, to examine, in an exploratory way, if Passive Acoustic Recorders (PAL) can detect sperm whale clicks. This was the first time PALs were used for this purpose. At deployments of remote autonomous passive acoustic recorders, issues of power supply, storage, duration, and recording frequencies, need to be considered. Compared to continuous acoustic recorders, PAL has an adaptive subsampling schedule that allows recording snapshots of the sound field when biological sound sources are identified. In this way, more synoptic data of wide bandwidth and high frequencies can be collected for longer periods, facilitating manual data analysis and assessments of temporal patterns and environmental drivers. Daily marine mammal presence is similar when recorded with a PAL or with a duty-cycled recorder (Denes et al., 2014). At the same time, efficient analysis of very large quantities of acoustic data is a challenging task. However, continuous recordings come with key advantages, and the use of subsampled data limits the research questions that can be investigated. Rare vocalizations of a certain species or detections of an acoustically cryptic species are more difficult to document when using a non-continuous recorder. Additionally, subsampled recordings can sometimes introduce a bias on classifying species and interpreting acoustic records, likely reducing the probability to detect targeted species and introducing an underestimation of species occurrence.

This study demonstrates that PAL is a cost-efficient tool, useful for the detection of acoustically dominant cetacean species. Using a common sampling strategy, sperm whales were continuously recorded at OSP, where this species is prevalent. The probability of the PAL detecting sperm whales remained high enough throughout the five-year deployment to allow quantification of the seasonal and interannual patterns of whale presence (Chapters 3 and 4). Since the Pylos station was much closer to the coast, where a variety of delphinid species occurs, sperm whale detections were much lower, yet were still reported every month of the year. At Athos, PAL recorded no sperm whales but also detected the almost continuous presence of what is believed to be largely Risso's dolphins. This species produces clicks with lower ICI and have a high probability of being detected by the PAL. To be able to confirm that sperm whales are absent from Athos, a PAL can be used with some adjustments to the classification algorithm. For instance, if we change the detection criteria to filter out signals with frequencies above 20 kHz, this allows more chances for sperm whale clicks to be recorded, if present. Thus, depending on the amount and diversity of vocal species present in an area, specific adjustments can be made to the PAL to detect more acoustic signals of interest.

Ultimately, the use of passive acoustic tools, including PAL, is a particularly effective methodology for studying cetacean ecology, and offers key benefits in the study of sperm whales. The important findings of this work are dependent on the use of long-term data sets that become possible with acoustic sampling methods. Acquiring additional data on sperm whale occurrence throughout the years increases our chances to detect ecological changes over time and monitor whale population dynamics and movements. Therefore, bioacoustic data can play a strategic role in the study of sperm whales and can be used to inform conservation efforts for the species. Having only one sampling station in each region is limiting our inferences related to migration patterns. A network of acoustic stations would provide a more complete assessment of the sperm whale distribution and movement patterns within certain basins. Ideally, a combination of research methods (acoustics, visual, and genetics) can be applied in the future in order to better understand the ecology of sperm whales and potential responses to global warming.

5.4 Thoughts for Conservation

People are using the seas and oceans of the world, often without consideration for its inhabitants. Anthropocentrism affects the welfare and survival of marine life. Shipping traffic has turned oceans into much louder places, which translates to increased stress levels for the whales (Rolland et al., 2012). Within the last 50 years, the number of commercial vessels transiting the world's oceans has at least doubled. Constant industrial development enhances the need for marine transports, and major seaways become ever denser, causing the increase of manmade ocean noise and the risk of ship strikes, particularly in the northern hemisphere. Though not exclusively, most anthropogenic activity is concentrated in coastal areas. Chemical pollution and litter introduce additional threats to the wellbeing of marine wildlife, as well as naval and fishing activities (Katsanevakis and Katsarou, 2004; Katsanevakis, 2008; Parsons, 2017).

Sperm whales and other marine organisms that are exposed to anthropogenic noise can be adversely affected on a short timescale (acute effect) and on a long time scale (chronic effects). To tackle these effects, in 2008 the European Commission, established the Marine Strategy Framework Directive (MSFD; Directive 2008/56/EC) and defined specific criteria and standards on the Good Environmental Status (GES) of marine waters (Commission Decision

2010/477/EU). Among the 11 descriptors of GES, the first refers to the state of biodiversity, and the last refers to underwater noise (Descriptor 11, Noise/Energy). Two indicators related to noise are included: low and mid frequency impulsive sounds (Indicator 11.1.1), and continuous low frequency sounds (ambient noise) (Indicator 11.2.1) (Van der Graaf et al., 2012). The shipping industry is willing to collaborate with scientists and environmentalists to comply with their requirements in order to protect marine wildlife. Specifically, the International Maritime Organization, (IMO), the UN agency that regulates the shipping industry, has passed new guidelines that include recommendations to make shipping quieter by targeting the noise source: the ships' propellers. However, a lack of data verifying the year-round presence of certain species can impede these efforts. The work in this dissertation contributes to the assessment of mean ambient sound levels and monitoring of year-round cetacean presence in the eastern Mediterranean Sea; a scientific effort that applies to both the biodiversity and the underwater-noise indicators of the MSFD, and the IMO requirements. Long-term passive acoustic recording is an excellent strategy for complying with the MSFD requirements for monitoring of marine life and ambient noise, and can ultimately contribute to their protection.

Besides the production of underwater noise, increased shipping traffic raises the possibility of ships and whales colliding. The risk of ship strike is likely the greatest threat that sperm whales face in the Greek Seas, accounting for more than 60% of whale deaths in the area. Ship strike concerns are focused at the Hellenic Trench, where the year-round sperm whale presence (Chapter 2) overlaps with major shipping lanes. Scientists suggest that with an offshore shift of the traffic, by about 10 km, the risk of collision would drop dramatically. Based on this idea, protection measures have been implemented successfully in many parts of the world. In 2004 at the Panama Canal, position of shipping lanes and vessel speed were changed in order to minimize overlap with humpback whale (Megaptera *novaeangliae*) migration routes. Similarly, in 2013 off the coast of California, shipping lanes were shifted further offshore to protect killer whales (*Orcinus orca*). For the protection of the critically endangered North Atlantic right whales, in August 2017, the Canadian government implemented a temporary mandatory slowdown for large vessels (>20 m) off Quebec, in the Gulf of St. Lawrence. Additional benefits occurring from ships' slowing down include the reduction of fuel consumption which also results in the decrease of gas emissions related to global warming.

Considering the year-round occurrence of sperm whales and delphinids at the Hellenic Trench, the oil exploration and construction activities along this zone in the Ionian Sea, planned by the Greek government is of growing concern. Besides the tremendous risk of a future oil spill and the dramatic consequences to the entire ecosystem, the increase of noise levels during the seismic surveys and due to higher densities of shipping traffic, can exacerbate the ecological impacts to cetaceans from other anthropogenic activities with multiple stressors operating as synergistic effects (Crain et al., 2008). In addition, as these explorations move offshore and into deeper water, the long-range propagation of seismic signals and the effects from noise reach the more pelagic ecosystems, which were before relatively more intact. Since 2017, the Agreement for the Conservation of Cetaceans of the Black and Mediterranean Seas (ACCOBAMS) has designated the Hellenic Trench as an Important Marine Mammal Area (IMMA). Since 2006, ACCOBAMS recognizes the urgency to create a Marine Protected Area (MPA) there, for the conservation of sperm and beaked whales. Results from this dissertation emphasize the importance of this area for sperm whales and other delphinids. The creation of an offshore MPA can help restrict oil exploration and drilling activities from an important habitat of an endangered species. A very recent example of successful efforts to prioritize sperm whale conservation in the Mediterranean comes from Spain, where in July 2018 the government established a 46.385 square kilometers protected reserve at the Balearic Sea. The Spanish state recognized the ecological value of an area that functions as a migration path for sperm whales and delphinids in the Western Mediterranean. By creating a marine wildlife reserve, the fossil fuel exploration in that area will be prohibited.

Lastly, for the GOA, a conservation concern is the proximity of OSP, and what appears to be a critical habitat for sperm whales, to an exercise area for the US Navy (TMAA). Thus, caution is required in order to avoid acoustic disturbance to the sperm whale population and avoid interrupting their feeding, since this site is likely a foraging ground (Chapter 3). With this work highlighting the potential ecological impacts to the Pacific sperm whale population due to ocean warming (Chapter 4), continuous acoustic monitoring can expand our understanding of these responses and allow for specific mitigation actions.

"For most of history, man has had to fight nature to survive; in this century he is beginning to realize that, in order to survive, he must protect it."

— Jacques-Yves Cousteau

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6. Appendix

6.1 APPENDIX A: Peer-reviewed articles

As output of this thesis, three articles were published in SCI journals, and two more congress proceedings:

(Published) Diogou N., H. Klinck, A. Frantzis, J. A. Nystuen, E. Papathanassiou, S. Katsanevakis. Year-round acoustic presence of sperm whales (*Physeter macrocephalus*) and baseline ambient ocean sound levels in the Greek Seas. Mediterranean Marine Science. *[Early view version, doi:http://dx.doi.org/10.12681/mms.18769].*

(Published) Diogou N., D. M. Palacios, J. A. Nystuen, E. Papathanassiou, S. Katsanevakis, H. Klinck. Sperm whale (Physeter macrocephalus) acoustic ecology at Ocean Station PAPA (Gulf of Alaska) – Part 1: detectability and seasonality. Deep-Sea Research Part I. Manuscript No: DSR1_2018_198.

(Published) Diogou N., D. M. Palacios, J. A. Nystuen, E. Papathanassiou, S. Katsanevakis, H. Klinck. Sperm whale (*Physeter macrocephalus)* acoustic ecology at Ocean Station PAPA (Gulf of Alaska) – Part 2: oceanographic drivers of interannual variability. *Deep-Sea Research Part I.* Manuscript No: DSR1_2018_199.

Conference Papers

Diogou N., Klinck, H., Oswald, J. N., Papathanassiou, E., Georgakarakos, S., and Nystuen, J. A., "Passive Acoustic Detections of Odontocetes in the Ionian and Aegean Seas, Greece", *Proceedings of Underwater Acoustics 2014*, pp. 1627-1632., **2014**.

Diogou N., J. Nystuen, E. Papathanassiou, S. Georgakarakos, "Preliminary results of the research for the presence of cetaceans in Greek Seas using passive acoustic monitoring (PAL)" *Proceedings of Panhellenic Symposium on Oceanography and Fisheries 10*, **2012.**

6.1 APPENDIX B: Presentations

Conference Presentations

Diogou N., Palacios D. M., Nystuen J. A., Papathanassiou E., Katsanevakis S., Klinck H. **(2017),** "Modeling the Environmental Drivers of Sperm Whale (Physeter macrocephalus) Multi-year Occurrence Patterns in the Gulf of Alaska", 22nd Biennial Conference for the Marine Mammals, Halifax, Nova Scotia, Canada. *Poster presentation*.

Diogou, N. (**2016**). "Interannual variability in sperm whale acoustic occurrence at Ocean Station PAPA from 2007-2012 related to oceanography", Ocean Station PAPA 60th Anniversary Symposium, Sidney, British Columbia, Canada. *Poster presentation.*

Diogou N., Klinck H., Nystuen J., Palacios D. (**2016**). "What whales want. The long term acoustic presence of sperm whales offshore in the Gulf of Alaska and their relationship to oceanographic conditions ". SMM-NW Student Chapter, Seattle, WA, USA. *Oral Presentation*.

Diogou N., Klinck H., Nystuen J., Palacios D. (**2015**). "Sperm whale (*Physeter macrocephalus*) acoustic occurrence patterns in the Gulf of Alaska and their environmental drivers", 21st Biennial Conference for the Marine Mammals, San Francisco, USA. *Poster presentation.*

Diogou N. (**2015**). "Passive acoustic recordings of sperm whale (*Physeter Macrocephalus*) presence at Ocean Station PAPA over six years ", Five-year review of the Cooperative Institute for Marine Resources, Oregon State University and NOAA Pacific Marine Environmental Laboratory, Newport, Oregon, USA. *Poster presentation*.

Diogou N., Papathanassiou E., Nystuen J, Katsanevakis S., Klinck H. (**2015**). "Acoustic presence of sperm whales *(Physeter macrocephalus)* and delphinids in the Ionian and Aegean Seas, Greece", Integrated Marine Research in the Mediterranean and the Black Seas, PERSEUS, Brussels, Belgium. *Poster presentation*

Diogou N., Klinck, H., Oswald, J. N., Papathanassiou, E., Georgakarakos, S., and Nystuen, J. A. (**2014**). "Passive Acoustic Detections of Odontocetes in the Ionian and Aegean Seas, Greece", Underwater Acoustics Conference, Island of Rhodes, Greece. *Poster presentation*.

Diogou N. (**2014**). "The acoustic presence of sperm whales (*Physeter macrocephalus*) at Ocean Station PAPA in the Gulf of Alaska 2007-2012". SMM-NW Student Chapter, Bellingham, WA. *Oral Presentation*.

Diogou, N., Klinck, H., Nystuen, J.A. (**2013**). "The acoustic presence of sperm whales (*Physeter macrocephalus*) at Ocean Station PAPA in the Gulf of Alaska 2007-2012". Acoustical Society of America, San Francisco, CA, USA. *Oral Presentation*.

Diogou, N. (**2013**). "Seasonal and interranual variability of sperm whale (*Physeter macrocephalus)* presence in the Gulf of Alaska". SMM-NW Student Chapter, Seattle, WA, USA. *Oral Presentation*.

Diogou N., J. Nystuen, E. Papathanassiou, S. Georgakarakos, (**2012**). "Preliminary results of the research for the presence of cetaceans in Greek Seas using passive acoustic monitoring (PAL)" 10th Panhellenic Symposium on Oceanography and Fisheries, Athens, Greece. *Oral presentation*

Invited Seminars and Public Presentations

Hatfield Marine Science Center, Marine Mammal Institute Seminar Series: "What whales want. The long term acoustic presence of sperm whales offshore in the Gulf of Alaska and their relationship to oceanographic conditions". Oregon State University, Newport, Oregon, USA, **2016**

Cyprus Oceanographic Center: The use of Acoustics to monitor marine mammals. University of Cyprus, Nicosia, Cyprus. **2015**

Hatfield Marine Science Center, Science Seminar Series: "#SciCom: The Science – Social Media Connection", Newport, Oregon, USA. **2014**

American Cetacean Society, Oregon Chapter Monthly Science Seminar: "Do you speak whale", Newport, Oregon, USA. **2014**

American Cetacean Society, Oregon Chapter Naturalists' Seminar: "Marine Bioacoustics, Sounds in the Sea", Newport, Oregon, USA. **2013**

Hatfield Marine Science Center, CIMRS: "Three research scientific questions: My study". Newport, Oregon, USA. **2012**

Conference participation without presenting

21st SMM-NW Student Chapter, 6-7 May 2017, Vancouver, British Colombia, Canada. **2017**.

25 Years of PICES: Celebrating the Past, imagining the Future, Annual Meeting of the North Pacific Marine Organization, 2-13 November 2016, San Diego, USA. **2016**

20th SMM-NW Student Chapter, 2-3 May 2015, Corvallis, Oregon, USA. *Organizing committee and session chair*. **2015**.

168th Meeting of the Acoustical Society of America, 27–31 October 2014, Indianapolis, Indiana, USA. **2014**

Fifth International Workshop on Detection, Classification, Localization, and Density Estimation of Marine Mammals using Passive Acoustics, 21 -25 August 2011, Timberline Lodge, Mount Hood, Oregon, USA. **2011**

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