

Multi-Species Foraging Associations in the Hauraki Gulf

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Abstract

Multi-species foraging associations (MSFAs) are characterised by the joining of two or more species to feed on ephemeral prey patches. Demographic analysis provides valuable insight into species interactions in MSFAs, with compositions and affinities highlighting the different costs and benefits of associating, such as kleptoparasitism, predation risk, and shifting prey availability through the scattering/dispersal and herding behaviours of other predators. Here, we use a combination of demographic and activity budget analysis tools to investigate MSFA dynamics ($n = 179$) in the Hauraki Gulf surveyed between 2019 and 2021. Within MSFAs, eight unique clusters of species were found, with associations forming on the basis of prey type and movement and foraging ecology. Species exhibited distinct social affinities, reflecting foraging ecologies, seasonal prey availability and predator movements and migrations. Using activity budget analysis tools and group focal follows, we found that cluster influenced the proportion of time groups spent in various behavioural states, with planktivores, and planktivore cluster participants, spending more time actively foraging than piscivores and piscivore and multitrophic cluster participants. Using these activity budgets, we provide novel insights into the influence of predator composition (cluster) and season on group behaviours. To further this work, we developed a proof-of-concept artificial intelligence (AI) tool to automate the detection and classification of animals and behaviours from imagery with human-like accuracy. Resulting YoloV4 and ResNet-50 models indicate that species can be detected to a mean average precision of 93.6 - 99.6%, and behavioural classifiers to 30.7% - 97.1%. Model accuracy improved with image resolution, but not number of classifier layers, with accuracy further increasing with the number of trained objects (animals), iterations and epochs. AI models were thus proven to be useful for future analysis of behavioural data from drone footage.

Overall, this research provides a baseline of information and understanding of the complexity of MSFA dynamics with the current ocean state. As large marine animals reflect cumulative stressors in their environment, fine-scale drivers of MSFAs warrant further research, with long-term monitoring of MSFAs providing insight into the effects of future climate and human-mediated environmental changes in the Hauraki Gulf Marine Park.



Janet Helen Davis

1935 – 2017

This thesis is dedicated to my Grandma Janet who inspired my passion for diving, exploring and love for the ocean and all its inhabitants.

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Table of Contents

Abstract	ii
Acknowledgements	iv
Table of Contents	vi
List of Figures	ix
List of Tables	x
List of Appendices	xi
Glossary and Abbreviations	xii
Chapter 1 General Introduction	1
1.1 Foraging Behaviour.....	1
1.1.1 Foraging ecology and plasticity.....	1
1.1.2 Patchy prey.....	2
1.1.3 Cue use in marine predators.....	2
1.1.4 Foraging ecology.....	4
1.2 Multi-species Foraging Associations.....	7
1.2.2 Drivers of MSFA formation.....	7
1.2.3 Role of species within MSFAs.....	8
1.3 Marine predators as Indicators of Ecosystem Health.....	10
1.3.2 Marine predators as ocean sentinels.....	10
1.3.3 Ngā tohu o te Taio – Māori environmental indicators.....	11
1.4 The Hauraki Gulf - Tīkapa Moana - Te Moananui-ā-Toi.....	11
1.5 Drones in ecology.....	12
1.6 Artificial intelligence in ecology.....	13
1.7 Thesis Structure.....	15
Chapter 2 MSFA Dynamics and Composition	17
2.1 Introduction.....	17
2.2 Methodology.....	19
2.1.1 Study Location.....	19
2.1.2 Data collection.....	19
2.2.3 Data analysis.....	20
2.3 Results.....	22
2.4 Discussion.....	31
2.4.1 Factors influencing composition.....	31

2.4.2	Frequent attendees and MSFA clusters	34
2.4.3	Infrequent and non-attendees	35
2.4.4	Conclusion	37
Chapter 3	Group behaviours within MSFA events	38
3.1	Introduction	38
3.2	Methods	41
3.2.1	Behavioural observations	41
3.2.2	Activity budget calculation	43
3.2.3	Data analysis	43
3.3	Results	44
3.3.1	Individual species	44
3.3.2	Season	47
3.3.3	Cluster and species	50
3.4	Discussion	53
3.4.1	Influence of richness and diversity on behaviours:	53
3.4.2	Behavioural budgets of frequently attending species	55
3.4.3	Influence of season on activity budgets	55
3.4.4	Clusters	57
3.4.5	Next steps and concluding remarks	58
Chapter 4	Drones and Artificial Intelligence in Marine Ecology	60
4.1	Introduction	60
4.1.1	Drones in Marine Ecology	60
4.1.2	Artificial intelligence in Marine Ecology	61
4.2	Methodology	62
4.2.1	Study areas	62
4.2.2	Drone footage collection	62
4.2.3	Machine learning training and testing	63
4.2.4	Data analysis and evaluation metrics	71
4.3	Results	73
4.3.1	Model misidentifications	73
4.3.2	YoloV4 Model Results	76
4.3.3	ResNet-50 Model results	78
4.4	Discussion	81
4.4.1	Precision of species annotations	82
4.4.2	Interpretation of behaviours from imagery	84
4.4.3	Collecting footage	85
4.4.4	Automated image tagging	86

4.4.5 Future steps	86
4.4.6 Conclusions.....	87
Chapter 5 General Discussion.....	89
5.1 Overview	89
5.2 MSFA dynamics	90
5.3 Environmental influences	92
5.4 Limitations.....	95
5.5 Next steps	96
5.6 Conclusion	97
References.....	99
Appendices.....	137

List of Figures

Figure 2.1 Map of research area with MSFA events (•, n = 179) and departure locations (Ti Point and Viaduct Basin) labelled.	22
Figure 2.2 (a) Hierarchical clustering dendrogram and (b) non-metric MDS ordination of Bray-Curtis similarity of 179 presence-absence transformed MSFAs with SIMPROF one-way analysis overlaid.	24
Figure 2.3 MSFA attendance patterns (% of sightings) across seasons, by species (n = 22).....	26
Figure 2.4 Frequency of cluster occurrence (%) by season.	27
Figure 2.5 MSFA attendance patterns (% of sightings) across clusters (a – h), by species (n = 22).	28
Figure 2.6 The social network of species associations within MSFA events (n = 179 MSFAs).....	30
Figure 3.1 Box and whisker plot of the proportion of time frequently attending species (>5% MSFAs) spent foraging, active non-foraging, and non-active non-foraging within MSFA events (n = 179)..	46
Figure 3.2 The proportion of time frequently attending species (>5% MSFAs; for species codes and attendance see Table 2.1) spent foraging, active non-foraging, and non-active non-foraging within MSFA events by season (n = 4)..	49
Figure 3.3 The proportion of time frequently attending species (>5% MSFAs; for species codes and attendance see Table 3.4) spent foraging, active non-foraging, non-active non-foraging and absent within MSFA events across the eight clusters (a - h).	52
Figure 4.1 Stages involved in the training of the convolutional neural network (CNN) to detect target animals and behaviours from drone footage.....	65
Figure 4.2 Example of YoloLabel graphical user interface with bounding boxes and associated species and behaviour classifiers listed.....	66
Figure 4.3 Examples of still images captured from drone imagery illustrating the 17 behaviour classifiers used in CNN training (see table 4.3 for descriptions)..	68
Figure 4.4 Geometrical representations of (a) IOU, (b) precision and (c) recall.....	71
Figure 4.5 Example of true positive detection (>50% Intercept Over Union) from drone image showing ground truth (manual bounding box, red) and predicted (yellow) bounding boxes (areas of union) with the area of overlap (intercept, yellow) shaded.	72
Figure 4.6 Examples of misidentified objects during auto-classification corrections.....	74
Figure 4.7 Directionality dot plot of the number of corrected annotations per frame, for each video clip auto tagged.....	75
Figure 4.8 Accuracy (mAP) of the preliminary model (YoloV4) to detect behaviours of two cetacean and five seabird species with total number of objects used to train that classifier.	77
Figure 4.9 a) Accuracy and b) loss (prediction error) of ResNet-50 single species classifier model across training epochs.	80

List of Tables

Table 2.1 Summary statistics of species attendance within MSFA events (n = 179).....	23
Table 2.2 SIMPER analysis of the contribution of each species (%) to the similarity between MSFAs calculated from the Bray-Curtis Similarity index.....	25
Table 2.3 The number (degrees) of species co-occurring (associations) during MSFA events.....	29
Table 3.1 Overview of behaviours of cetaceans and seabirds within multi-species foraging associations.	42
Table 3.2 Fixed effects tested using GLM's.....	43
Table 3.3 Summary statistics (average \pm SE) of proportion of MSFA event spent in each behavioural state for frequently attending species.	45
Table 3.4 Summary of significant continuous GLM variables (diversity, duration and richness; $p < 0.05$) for frequently attending species (>5% MSFAs) for the behavioural states..	47
Table 3.5 Summary of significant pairwise comparisons ($p < 0.05$) of seasons (n = 4) by frequently attending species (>5% MSFAs) for behavioural states.....	50
Table 3.6 Summary of significant pairwise comparisons ($p < 0.05$) of seasons by cluster (n = 8) for behavioural states. First season listed has a greater (+) or lesser (-) proportion of time compared to the second season listed	51
Table 4.1 Artificial Intelligence terminology and definitions.....	64
Table 4.2 Grading system (1 - 4) and assessment criteria to evaluate drone image quality.....	65
Table 4.3 Seabird and cetacean CNN classifiers and behavioural descriptions.....	67
Table 4.4 Augmentations applied to this model.....	69
Table 4.5 Objects and mean Average Precision (mAP) for YoloV4 and ResNet-50 models for different species and behaviour classifiers	76

List of Appendices

Appendix 1 Social affinity index between species (for species codes see Table 2.1; n = 22).137

Appendix 2 Preliminary model Accuracy-Loss graph (mAP: 41.3%; layers: 53; Pixels: 1280 x 1280)
..... 138

Appendix 3 Preliminary model Accuracy-Loss Graph (mAP: 46.7%; Layers: 29; Pixels: 816 x 816).
.....139

Appendix 4 Preliminary model Accuracy-Loss Graph (mAP: 80.2%; Layers: 29; Pixels: 2016 x 1152).
.....140

Glossary and Abbreviations

(In order of appearance)

MSFA	Multi-species foraging association
Mātauranga Māori	Traditional knowledge of the Māori people of New Zealand, Aotearoa
Tikanga	Māori customary practices or behaviours
Tapu	Traditional concept denoting something holy or sacred, with spiritual restriction or implied prohibition.
Rāhui	A form of tapu restricting access to, or use of, an area or resource by the kaitiakitanga (guardians) of the area
Mataitai	Traditional management areas where the tangata whenua manage all non-commercial fishing by making bylaws
AWADS	Auckland Whale and Dolphin Safari
ARDBUL	Buller's shearwater, Rako, <i>Ardenna bulleri</i>
ARDCAR	Flesh-footed shearwater, Toanui, tuanui, <i>Ardenna carneipes</i>
ARDGRI	Sooty shearwater, Tītī, <i>Ardenna griseus</i>
BALBRY	Bryde's whale, <i>Balaenoptera edeni brydei</i>
DELDEL	Common dolphin, <i>Delphinus delphis</i>
EUDMIN	Northern little (blue) penguin, Kororā, <i>Eudyptula minor</i>
LARDOM	Southern black-backed gull, Karoro, <i>Larus dominicanus</i>
LARNOV	Red-billed gull, Tarāpunga, <i>Larus novaehollandiae</i>
MACHAL	Northern giant petrel, pāngurunguru, <i>Macronectes halli</i>
MORSER	Australasian gannet, Tākapu, tākupu, <i>Morus serrator</i>
PACTUR	Fairy prion, Tītī wainui, <i>Pachyptila turtur</i>
PELURI	Common diving petrel, Kuaka, <i>Pelecanoides urinatrix</i>
PHAVAR	Pied shag, Kāruhiruhi, kawau, <i>Phalacrocorax varius</i>
PROPAR	Black petrel, tākoketai, <i>Procellaria parkinsoni</i>
PTECOO	Cook's petrel, Tītī, <i>Pterodroma cookii</i>
PTEGOU	Grey-faced petrel, Ōi, Tītī, <i>Pterodroma gouldi</i>
PUFGAV	Fluttering shearwater, Pakahā, <i>Puffinus gavia</i>
STESTR	White-fronted tern, Tara, <i>Sterna striata</i>
STOPET	New Zealand storm petrel, <i>Fregatta maoriana</i> and White-faced storm petrel, Takahikare–moana, takahikare, <i>Pelagodroma marina</i>
TURTRU	Bottlenose dolphin, <i>Tursiops truncatus</i>
GPS	Global Positioning System
SIMPER	Similarity Percentages Analysis
GLM	Generalised Linear Model

AI	Artificial intelligence
ML	Machine Learning
CNN	Convolutional Neural Network
GUI	Graphical user interface
mAP	Mean Average Precision
IoU	Intercept over Union

Chapter 1 General Introduction

1.1 Foraging Behaviour

1.1.1 Foraging ecology and plasticity

Foraging is a term used to describe the traits and behaviours used by an individual to detect, search for, and obtain food. Foraging ecology describes an individual's foraging behaviours, prey specificity and spatial distribution. These actions, solitary or in groups, have evolved to maximise individual foraging success and energetic gains while minimising costs under environmental changes and competition (Marshall & Pyenson, 2019; Sheppard *et al.*, 2021; Sotillo *et al.*, 2019). Within populations of generalist foragers, there are often specialist individuals (Bolnick *et al.*, 2007), with differences in personality and prey specificity reducing foraging competition (S. Harris *et al.*, 2020; Patrick & Weimerskirch, 2014; Waugh & Weimerskirch, 2003). Populations and individuals can adopt generalist or specialist foraging behaviours depending on prey availability and suitable habitats (Waugh & Weimerskirch, 2003).

Species that exclusively forage in particular habitats or have restricted prey preferences are vulnerable to anthropogenically driven bottom-up shifts in prey abundance and habitat structure (Divoky *et al.*, 2021; Mery & Burns, 2010). Foraging plasticity maximises efficiency in novel, unpredictable, patchy, and disturbed habitats while minimising fitness costs (Gilmour *et al.*, 2018; Snell-Rood, 2013). Species modify their behaviour in response to changes in environmental conditions and external and internal stimuli - including sociality, prey availability, predator presence and cooperation (Gomes & Cardoso, 2020; Rodríguez-Prieto *et al.*, 2011). An individual's ability to adjust their foraging behaviours affects their life history through reproductive success (Chiaradia & Nisbet, 2006), mate choice (Barou-Dagues *et al.*, 2020), and habitat selection (Manenti *et al.*, 2013). However, flexibility can be constrained by morphology, physiology, memory (Bélisle & Cresswell, 1997; Camprasse *et al.*, 2017; De Pascalis *et al.*, 2020) and breeding and moulting limitations (Lamb *et al.*, 2020; Rayner *et al.*, 2017; Russell *et al.*, 2015). Shifts in prey availability create trophic cascades up food webs; thus, the temporal and spatial distribution of high-trophic level predators can be used as sensitive indicators and proxies of changing prey distribution and availability (Boyd & Murray, 2001; Carroll *et al.*, 2017; Hazen *et al.*, 2019). Predator-prey models provide insights into the health of large marine animals' habitat and ecosystem, with density-dependent factors influencing population dynamics and species distribution, sometimes making them climate and ecosystem sentinels (Hazen *et al.*, 2019; van den Berg *et al.*, 2021).

1.1.2 Patchy prey

Oceanographic habitats and biophysical processes, such as the El Niño Southern Oscillation, sea surface temperatures and primary productivity, are attributed to shifts in the spatiotemporal distribution, abundance, and diversity of marine prey (Cox *et al.*, 2018; Sprogis *et al.*, 2018; Weimerskirch *et al.*, 2005). Oceanographic conditions influence the abundance and distribution of primary producers and intermediate trophic links (e.g., zooplankton and small schooling fishes), with primary production providing a holistic overview of ecosystem productivity (Anderwald *et al.*, 2012; Laidre *et al.*, 2003; Pulliam, 1974; Suryan *et al.*, 2012). Prey concentration at 'hotspots' increases foraging efficiency for top predators through improved prey detection and capture success (Burgess, 2006; Cox *et al.*, 2018; Hastie *et al.*, 2004). For example, baleen whales form super-groups at prey hotspots, collectively working to detect high biomass, low-trophic level, increasing individual prey capture success (Cade *et al.*, 2021; van Someren Gréve *et al.*, 2019). Likewise, filter-feeding whale sharks (*Rhinocodon typus*; Boldrocchi & Bettinetti, 2019; Heyman *et al.*, 2001), basking sharks (*Cetorhinus maximus*; Crowe *et al.*, 2018) and manta rays (*Mobula alfred*; Armstrong *et al.*, 2016; Harris *et al.*, 2021) aggregate in productive prey hotspots to feed on high-density fish spawn, small fish, and surface plankton blooms.

1.1.3 Cue use in marine predators

Information transfer involves individuals acquiring information from cues emitted by conspecifics (Dall *et al.*, 2005; Goodale *et al.*, 2010). This process results in local enhancement, whereby visual, chemical, and auditory cues enhance the local environment, increasing foraging efficiency for predators by improving the detectability of ephemeral and spatially dynamic prey (Page & Bernal, 2020; Thiebault *et al.*, 2014; Torres, 2017). Responsiveness to cues is species-specific and dependent on foraging conditions such as prey preference, density, and availability (Bairos-Novak *et al.*, 2015; Rouviere & Ruxton, 2022). Information transfer is helpful for group-living animals, with group decisions made using both public and private information (Falcón-Cortés *et al.*, 2019; King & Cowlshaw, 2007; Weimerskirch *et al.*, 2010). Both marine and terrestrial predators may use conspecifics (Bairos-Novak *et al.*, 2015), olfactory cues (Dell'Aricecia *et al.*, 2014; Nevitt, 2008; Orlando *et al.*, 2020) and social information transfer within communities to detect prey (Boyd *et al.*, 2016; C. Jones *et al.*, 2020). These cues often drive the attraction and assemblage of species across multiple trophic levels to the same ephemeral prey patch, leading to the formation of multispecies feeding aggregations (MSFAs) (Fauchald, 2009; Griffin *et al.*, 2005; Lukoschek & McCormick, 2000; Nevitt & Bonadonna, 2005).

Olfaction cue use is species-specific and dependent on predators' ability to detect the cue and the concentration of scents and chemicals (DeBose & Nevitt, 2008; Nevitt *et al.*, 2004, 2006; Savoca & Nevitt, 2014). Many seabird species, including Procellariiformes (Dell'Aricecia *et al.*, 2014; Nevitt, 2008) and penguins (Amo *et al.*, 2013; Wright *et al.*, 2011), use dimethyl-sulphide (DMS), a chemical

produced by grazing herbivores, to detect patchily distributed prey (Amo *et al.*, 2013; Cunningham *et al.*, 2009; Dacey & Wakeham, 1986; Nevitt, 2008; Savoca & Nevitt, 2014). However, the use of DMS is not well understood for marine mammals. Olfaction cue use in marine mammals is dependent on morphology and prey preference, reflecting trade-offs between respiratory and olfactory functions and foraging ecology (Kishida, 2021; Van Valkenburgh *et al.*, 2011). Foraging behaviours by baleen whales suggests they utilise DMS to locate prey aggregations and navigate at sea, yet in toothed cetaceans, DMS use is unclear (Bouchard *et al.*, 2019, 2022; Torres, 2017).

Visual cues of feeding events are dependent on the aggregation height, density and presence of conspecifics or those with similar foraging ecologies (Bairos-Novak *et al.*, 2015; Tremblay *et al.*, 2014). Species which rely on visual cues are vulnerable to shifts in the optical water conditions, with visual ranges and predator-prey interactions affected by eutrophication and sedimentation (Lukies *et al.*, 2021; Ranåker *et al.*, 2012). Thus, seasonal and anthropogenic shifts in optical conditions affect foraging conditions, with increased turbidity reducing near-surface prey detectability, accessibility and capture success (Holbech *et al.*, 2018; Lukies *et al.*, 2021). Likewise, aggregation size influences an individual's reaction distance and decision to join and forage within MSFA events, with size acting as a proxy of prey presence and foraging conditions (Thiebault *et al.*, 2014; Ruxton & Johnsen, 2016). Surface foraging by cetaceans is highly visible, with surface splashing and herding of prey to the surface acting as visual cues to seabirds, facilitating the formation of MSFA events (Clua & Grosvalet, 2001; Vaughn *et al.*, 2008; Würsig & Würsig, 1980). Prey herding behaviours further increase the visibility and accessibility of prey to near-surface foragers (Harrison *et al.*, 1991; McInnes & Pistorius, 2019; R. Vaughn *et al.*, 2010).

Olfactory and visual cues are limited for sub-surface predators. Thus, acoustic cues can be an essential driver of predator-prey dynamics in the ocean, conveying vital information on the surrounding environment (Au & Hastings, 2008; Montgomery & Radford, 2017; Putland *et al.*, 2016, 2019). Sound is essential for all kinds of marine species, with biological sound driving larval fish and crustacean movement and settlement (Radford *et al.*, 2011; Stanley *et al.*, 2011), communication and social cohesion (Van Oosterom *et al.*, 2016), and navigation (Au, 1993; Torres, 2017; Zapetis & Szesciorka, 2018). Eavesdropping on hetero-, conspecific and environmental cues enhance prey detection and group coordination, with acoustic cues acting as indicators of prey availability (Dawson, 1991; Götz *et al.*, 2006; Holt & Johnston, 2011). Many cetaceans use echolocation and vocalisations to communicate and coordinate foraging, detect, and alter prey behaviour, and localise items in 3D spaces (e.g., Au, 2018; Simon *et al.*, 2006; van Opzeeland *et al.*, 2005; Zapetis & Szesciorka, 2018). Acoustic cues produced by MSFA attendees drive the attraction of conspecifics and heterospecifics to exploit prey patches (Montgomery & Radford, 2017; Putland *et al.*, 2016). During dives, seabirds can eavesdrop on surrounding predators and prey, enhancing individual foraging success (K. Hansen *et al.*, 2017, 2020; Sørensen *et al.*, 2020). Vocalisations during underwater feeding may further

coordinate group foraging activities, with auditory cues enhancing foraging success in crowded prey patches (K. Hansen *et al.*, 2020; Thiebault, *et al.*, 2019).

1.1.4 Foraging ecology

Morphology

Air-breathing marine animals that exist in both terrestrial and marine environments experience morphological and behavioural trade-offs. These trade-offs influence the strategies used to overcome buoyancy and hydrodynamic drag when diving and swimming (Cook *et al.*, 2010; Elliott *et al.*, 2007; Hays *et al.*, 2004; Sato *et al.*, 2013). Many marine predators make extensive foraging trips from the surface to below 200m, using buoyancy and behavioural adjustments to optimise the cost of transport and efficiently forage at great depths (Elliott *et al.*, 2007; Gleiss *et al.*, 2011, 2013; Sato *et al.*, 2013). Bill morphology and size further affects prey selectivity and the trophic level seabirds can target, with longer and broader bills in plunge-divers reducing drag while diving (Crandell *et al.*, 2019; Eliason *et al.*, 2020). Foraging ecology is also influenced by the ability to capture prey, with covariation evident between tooth shape and diet in sharks (Bazzi *et al.*, 2021) and piscivorous fishes (Carr & Motta, 2020). Likewise, baleen whales filter-feed on densely aggregated low trophic level prey, whereas odontocetes use echolocation to assist prey capture with their teeth (Au, 1993, 2009; Goldbogen *et al.*, 2011, 2017; Goldbogen & Madsen, 2018). Filter-feeding marine animals are limited to feeding on low trophic level species, such as schools of small fishes and zooplankton patches, with foraging enhanced through lunge feeding into prey aggregations (Armstrong *et al.*, 2021; Croll *et al.*, 2018; Shadwick *et al.*, 2019). Filter-feeding seabirds use unique palatal lamellae to sieve prey from the water, with fewer filtering lamellae attributed to the targeting of higher trophic level prey (C. Jones *et al.*, 2020; Klages & Cooper, 1992).

Foraging niche partitioning

Niche partitioning is reflected in the temporal dynamics of foraging, with foraging behaviours often reflecting diel migration of preferred prey (Benoit-Bird *et al.*, 2009; Bentley *et al.*, 2021; Lee *et al.*, 2015; Wilson *et al.*, 1993). Among cetaceans, the diel availability of preferred prey may influence foraging behaviours. Vertical prey movement is associated with increased nocturnal foraging activity and diving depths in long-finned pilot whales (*Globicephala melas*) and sperm whales (*Physeter macrocephalus*) (Amano & Yoshioka, 2003; Baird *et al.*, 2002). Conversely, Bryde's whales (*Balaenoptera edeni brydei*) favour resting and reduced diving at night (Izadi *et al.*, 2018). In sympatric species, habitat segregation facilitates foraging niche partitioning, minimising competition for limited resources (Gavrillchuk *et al.*, 2014; Gulka *et al.*, 2019). Among large pelagic predatory fishes, habitat variation facilitates niche partitioning, with nutrient and prey limitations driving species to exploit different prey (Dwyer *et al.*, 2020; Matich *et al.*, 2017; Varghese *et al.*, 2014). However, in pinnipeds, dietary niche segregation is attributed to biomechanics and feeding morphology, such as bite force and gape (Drago *et al.*, 2017; Franco-Moreno *et al.*, 2021).

Sexual dimorphism can drive further niche partitioning, with cetaceans often exhibiting spatial and dietary differences between sexes (i.e., killer whales (*Orcinus orca*, Beerman *et al.*, 2016); beluga whales (*Delphinapterus leucas*, Szpak *et al.*, 2020; Narwhals (*Monodon monoceros*, Louis *et al.*, 2021). In pelagic seabirds, sex-based foraging differences are reflected in giant petrels (*Macronectes* spp.) and wandering albatrosses (*Diomedea exulans*), with females travelling further than males. Scavenging seabirds, however, show varied responses, with some males utilising fisheries discards (Stauss *et al.*, 2012; Zango *et al.*, 2020) and foraging more distantly from nesting areas in respect to females (Camphuysen *et al.*, 2015). Sexual dimorphism and sex-related differences in foraging are particularly evident among pinnipeds, with sexual segregation evident in both trophic positions and foraging ranges (Campagna *et al.*, 2021; K. Jones *et al.*, 2020; Page *et al.*, 2005).

Central place foragers experience breeding-associated foraging limitations as they must return to their nest to care for offspring (Orians, 1979). Seabird reproduction is characterised by long periods of biparental care, with both parents helping to incubate and feed chicks, adapting foraging efforts to their chick and partner's needs (Gillies *et al.*, 2021; Johnsen *et al.*, 1994). For seabirds, sharing incubation duties allows both parents to maintain body condition during chick raising, with one staying with the chick while the other forages (Burke & Montevecchi, 2009; Cohen *et al.*, 2014). As chicks develop and increase their demand for food, parent seabirds must also adapt to sufficiently provide for their chicks, increasing their foraging range, and diving and foraging efforts (Rayner *et al.*, 2010; Zimmer *et al.*, 2011). As the chick becomes bigger and less susceptible to predation, the 'post-guard' phase allows both parents to forage and leave the chick alone for extended periods. Parents can show increased resource partitioning during post-guard to cope with increased energetic demands and reduce competition with sympatrically breeding birds (Barger *et al.*, 2016; Botha & Pistorius, 2018). When near-nest prey availability decreases, parent seabirds target higher trophic level prey, further from nesting sites, highlighting the importance of prey accessibility and abundance in dynamic ecosystems (Dunphy *et al.*, 2020).

Movement

The movement ecology of marine animals is influenced by their specific life histories, movement capacity, and resource distribution and competition (Frankish *et al.*, 2020; Hays *et al.*, 2016; Rohner *et al.*, 2020). Movements include long trans-equatorial and inter-oceanic migrations between breeding and foraging grounds (González-Solís *et al.*, 2007; Rohner *et al.*, 2020; Williams *et al.*, 2006). Many seabirds are efficient migrators, undertaking trans-equatorial migrations to seek out productive areas, avoiding cooler winter months in both hemispheres (Shaffer *et al.*, 2006). These migrations are concurrent with prevailing wind patterns and coastal upwelling systems, allowing seabirds to save energy while migrating, and maximise prey access in destinations (González-Solís *et al.*, 2007; Weimerskirch *et al.*, 2000). Non-migratory seabirds, however, forage in a relatively small areas and are vulnerable to localised depletions in prey availability, with prey depletion being

reflected in breeding success and adult health (Kowalczyk *et al.*, 2015). Many cetaceans undertake annual migrations from summer polar feeding grounds to winter tropical breeding grounds (Corkeron & Connor, 1999). Fine-scale movement variation is observed within and between sympatric species, with foraging ranges resulting in spatial and temporal dietary partitioning and reduced resource competition (Kappes *et al.*, 2011; Navarro *et al.*, 2013; Regular *et al.*, 2011). Fine-scale movement allows seabirds to avoid competitive exclusion and kleptoparasitism by heterospecifics, such as predatory fish and aggressive seabirds (Hoffman *et al.*, 1981; Piatt, 1990; Sutton *et al.*, 2020). This spatial niche partitioning is reflected in black-backed gulls' (*Larus marinus*) and herring gulls' (*Larus argentatus*) narrow isotopic niches, with offshore colonies targeting higher trophic level prey compared to inshore colonies (Maynard & Davoren, 2020). While some species migrate as coordinated groups, others migrate independently and associate in destinations or *en route* during feeding and socialising (Colbeck *et al.*, 2013; Valsecchi *et al.*, 2002). Long-term movements along migration corridors are exhibited in sharks, with many species showing site philopatry and aggregation at breeding grounds (Bonfil *et al.*, 2005; Grubbs *et al.*, 2007; Kadar *et al.*, 2019). In pinnipeds, however, associations and habitat preferences reflect temporary aggregations during breeding seasons and seasonal shifts in habitat suitability (Chilvers & Dobbins, 2021; Procksch *et al.*, 2020).

Extensions of foraging ranges and spatial ranges allows animals to cope with environmental stochasticity, extending foraging ranges and excursions to undertake energetically demanding foraging trips to maximise prey capture success and energy delivery (Paiva *et al.*, 2013; Ricklefs, 1983; Stephenson *et al.*, 2020, in review). Prey density and habitat conditions, such as rainfall and luminosity, further influence elasmobranchs' spatial distribution and habitat use (Heupel *et al.*, 2018; Niella *et al.*, 2021). By showing diel and spatial variability in foraging, competition for similar prey between sympatric species can be reduced (Almeida *et al.*, 2021; Damseaux *et al.*, 2021; Lear *et al.*, 2021).

Oceanographic conditions

Shifts in oceanographic conditions, such as sea surface temperature and water clarity, indirectly drive changes in marine predators' distribution through shifting the spatial and temporal distribution of low-trophic level prey (Cox *et al.*, 2018; Embling *et al.*, 2012; Fauchald, 2009; Santora *et al.*, 2017; Stephenson *et al.*, in review). Seasonal shifts in prey abundance, oceanic and habitat conditions correlate with cetacean and seabird migrations, with many species predictably aggregating in breeding and feeding grounds (Chambault *et al.*, 2018; Gill *et al.*, 2011; Laidre *et al.*, 2008). Many cetaceans migrate between productive polar feeding grounds and warm low latitude breeding grounds using migratory corridors (e.g., Constantine *et al.*, 2007; Renault-Braga *et al.*, 2021). Seasonal shifts in habitat use are also evident, with foraging range extending when preferred prey was less abundant (Wedekin *et al.*, 2007). Large marine animals show non-linear behavioural and movement responses to shifts in prey availability and distribution driven by changes in biophysical

ocean characteristics (Benoit-Bird *et al.*, 2013; Dunphy *et al.*, 2020; Waggitt *et al.*, 2016). Foraging plasticity and opportunistic feeding are evident in local contexts, whereby reductions in preferred prey results in shifts in observed foraging strategies and prey selection (Gaglio *et al.*, 2018a; Kienle *et al.*, 2020).

Animal interactions

Social information transfer is helpful for group-living animals, as decisions are made using personal and public information (Falcón-Cortés *et al.*, 2019; King & Cowlshaw, 2007; Weimerskirch *et al.*, 2010). Facilitative interactions and social learning create positive associations between species, with some taxa becoming dependent on facilitation by others (Camphuysen & Webb, 1999; Goyert *et al.*, 2014; Pöysä, 1992). Commensalism provides heterospecifics with increased foraging opportunities, often at little to no cost to other species. Commensalism and mutualism occur across foraging taxa, with foraging by one species facilitating prey access for another (Boucher *et al.*, 1982; Bulleri *et al.*, 2016; McInnes & Pistorius, 2019; Rodríguez *et al.*, 2019; Stachowicz, 2001). Mutualistic strategies, such as interactions between sub-surface and aerial predators, can create tight aggregations of prey, increasing accessibility for both predators (Gatti *et al.*, 2021; McInnes & Pistorius, 2019; Vaughn *et al.*, 2010). However, not all interactions are beneficial. Aggression, predation and kleptoparasitism may drive species to avoid interactions. Kleptoparasitism is common among seabirds and refers to food-stealing within and between species, with one individual aerially chasing and stealing food from another (Brockmann & Barnard, 1979; Gaglio *et al.*, 2018b; García *et al.*, 2010; Machovsky-Capuska *et al.*, 2011a). Negative interactions are further shown between marine mammals and sharks, with predation risk, fear and competition shaping habitat use decisions (Courbin *et al.*, 2022; Heithaus & Dill, 2006; Wirsing *et al.*, 2007).

1.2 Multi-species Foraging Associations

1.2.2 Drivers of MSFA formation

MSFAs increase foraging efficiency for various social foragers and scavengers with the facilitation of foraging outweighing prey competition costs (Goodale & Nieh, 2012; Goyert *et al.*, 2018a; Thiebault *et al.*, 2016; Vaughn *et al.*, 2007, 2008). Marine animals benefit from MSFAs by generating 'information centres', allowing unsuccessful foragers to follow others to patchily distributed prey aggregations, increasing foraging success (Götmark *et al.*, 1986; Weimerskirch *et al.*, 2010). Rapid information transfer through visual, auditory, or olfactory cues allows predators to aggregate rapidly at ephemeral prey patches (Pöysä, 1992; Silverman *et al.*, 2004). Species within MSFAs tend to exhibit social fluidity and loose social groupings depending on the foraging conditions, balancing social and energetic demands to maximise foraging success (Cansse *et al.*, 2020; Stensland *et al.*, 2003). These MSFAs thus play a role in structuring communities and facilitating predator-prey dynamics (Ballance *et al.*, 1997; Hunt Jr, 1990; Porter & Sealy, 1982).

Splashing prey, diving seabirds and echolocating cetaceans provide auditory and visual cues for other species, promoting avoidance of predators, prey detection and the formation of MSFAs (e.g., Benti *et al.*, 2021; Putland *et al.*, 2016). Cooperative foraging within these multi-predator assemblages increases individual foraging success (Sutton *et al.*, 2020) and prey access (Cansse *et al.*, 2020; Goyert *et al.*, 2014; Goyert *et al.*, 2018a; McInnes & Pistorius, 2019), whilst group foraging reduces predation risk (Anderwald *et al.*, 2012; Chilton & Sealy, 1987; Thiebault *et al.*, 2016; Waggitt *et al.*, 2016). Seabirds take advantage of sub-surface predator foraging activity when prey is made available at the water's surface through herding behaviours, leading to enhanced foraging efficiency (Anderwald *et al.*, 2011; Jaquemet *et al.*, 2004; Vaughn *et al.*, 2008).

Primary productivity and associated predator aggregations are driven by bathymetric characteristics of habitats and associated seasonal upwelling of nutrient-rich waters (Copping *et al.*, 2018; Kent *et al.*, 2020). Primary productivity supports low trophic level species such as zooplankton and juvenile fish, which attract species at various trophic levels to the same foraging hotspot (Ballance *et al.*, 1997; Cox *et al.*, 2018; Gaskin & Rayner, 2013). For example, schools of piscivorous fishes, such as trevally (*Pseudocranax dentex*) and kahawai (*Arripis trutta*), herd these low trophic level species up to the surface, further increasing the accessibility of prey to seabirds (Gaskin & Rayner, 2013). Subsurface predators, such as tuna and dolphins, drive prey to the surface, enhancing prey detection and accessibility for surface feeding predators (Bräger, 1998; Degradi *et al.*, 2014; Evans, 1982; Scott *et al.*, 2012). Likewise, sub-surface predators benefit from joint feeding with prey herding heterospecifics and supplemented food such as fisheries discards and carcasses (Gallagher *et al.*, 2018; Heithaus, 2001; Jourdain & Vongraven, 2017; Stockin & Burgess, 2005; Svane, 2005). Supplemental fishing-related food sources for marine predators include discards, offal and fish protruding through the netting (Bugoni *et al.*, 2010; Maynard *et al.*, 2020; Svane, 2005). Associations with fishing vessels indicate natural prey availability, with supplemental feed modifying predator-prey interactions and contributing to unbalanced communities exploiting the same prey patches (Bicknell *et al.*, 2013; Bugoni *et al.*, 2010).

1.2.3 Role of species within MSFAs

MSFA foraging benefits are dependent on whether species are 'followers' or 'leaders', foraging competition, and the timing of arrival to the MSFA event (Camphuysen, 2006; Sridhar *et al.*, 2009). Species take on various roles within foraging aggregations, with gregariousness (Sridhar & Shanker, 2014), boldness (Dyer *et al.*, 2009; Kurvers *et al.*, 2010), vulnerability and size (Sridhar *et al.*, 2009) determining the foraging hierarchy, role, behaviours, and foraging success of individuals (Torres Ortiz *et al.*, 2021). Dominant species display kleptoparasitism, whereby heterospecifics gain energy from stealing food directly from another predator (Corre & Jouventin, 1997; Vickery & Brooke, 1994). Large marine animals, such as cetaceans and predatory fish, often facilitate MSFAs through concentrating

prey patches and generating foraging cues (Clua & Grosvalet, 2001; Cox *et al.*, 2018; Gatti *et al.*, 2021; McInnes & Pistorius, 2019; Vaughn *et al.*, 2010). In the central-eastern Pacific, seabirds, including boobies (Sulidae), shearwaters (Procellariidae) and skua/jaegers (Stercorariidae), forage alongside prey-herding tuna (*Thunnus albacares*) and spinner (*Stenella longirostris*) and spotted (*Stenella attenuata*) dolphins (Au & Pitman, 1986; Ballance *et al.*, 1997; Weimerskirch *et al.*, 2008). In the Azores, bottlenose (*Tursiops truncatus*), common (*Delphinus delphis*), and spotted dolphins forage together in MSFAs, with shared herding increasing foraging efficiency (Clua & Grosvalet, 2001; Quérouil *et al.*, 2008). Dolphins take on distinct roles during MSFA events, with collective labour increasing prey accessibility and maintaining prey aggregations (Gazda *et al.*, 2005; Mann *et al.*, 2000; Weiss, 2006). Herding passes of dolphins above or below prey balls act to concentrate prey, with more frequent prey capture attempts occurring in larger prey patches (Vaughn-Hirshorn *et al.*, 2013; Vaughn *et al.*, 2011). Feeding associations also develop between heterospecifics, with near-surface foraging seabirds observed foraging alongside sub-surface predators, which drive prey to the surface (Camphuysen & Webb, 1999; Harrison *et al.*, 1991; Le Corre & Jaquemet, 2005; Silverman *et al.*, 2004). Seabirds also respond positively to conspecifics, using local enhancement and predator aggregations to detect ephemeral prey patches (Bairros-Novak *et al.*, 2015; Thiebault *et al.*, 2014). Not all seabird species have the same roles within MSFAs; some seabirds dissipate groups, whereas others keep prey close to the surface, prolonging MSFA duration (Mills, 1998). Pursuit diving seabirds are considered necessary maintainers of feeding aggregations, driving prey to the surface, increasing accessibility for other birds (Grover & Olla, 1983; McInnes & Pistorius, 2019). However, diving seabirds may exert a vertical scattering effect on prey patches, dispersing the prey (Hulsman & Tularam, 2021; Purvin, 2015).

These associations also include predatory fish, such as tuna and seabass, which have similar herding behaviours to cetaceans, increasing prey availability to seabirds (Au & Pitman, 1986; Clua & Grosvalet, 2001; Gatti *et al.*, 2021; Scott *et al.*, 2012). Among elasmobranchs, MSFA roles vary with foraging behaviours. Whale sharks and manta rays feed on small fish and myctophids in the presence of other predators, which concentrate prey into easily accessible patches, with filter feeders ram feeding and vertical feeding on prey (Lester *et al.*, 2022). Symbiotic remoras (*Remora remora*) are also found to forage alongside their hosts, foraging from the same MSFA prey patch (Solleliet-Ferreira *et al.*, 2020). In some communities, large predators will terminate the workup by consuming large amounts of food, such as the lunge-feeding behaviours of baleen whales (Burgess, 2006; Haynes *et al.*, 2011; Izadi *et al.*, 2022).

1.3 Marine predators as Indicators of Ecosystem Health

1.3.2 Marine predators as ocean sentinels

Wide-ranging, long-lived, slow reproducing marine species provide valuable indications of anthropogenic stressors and diseases (Bossart, 2011; Domiciano *et al.*, 2017; Hazen *et al.*, 2019; Thibault *et al.*, 2019). Stressors on marine predators may be direct, such as habitat loss or loss of associated species, or indirect, including bottom-up trophic cascades driven by shifts in primary productivity or climate change (Bond & Lavers, 2014; Laidre *et al.*, 2015; Lukies *et al.*, 2021; Williamson *et al.*, 2021). Low fecundity increases vulnerability to anthropogenic mortality threats, further impacting those with small or recovering populations (e.g., Constantine *et al.*, 2015; Dias *et al.*, 2019; Stevens *et al.*, 2000). Maternal investments, such as long lactation duration, allomaternal care and social learning transmission, make many female cetaceans and pinnipeds susceptible to oceanographic stressors and reduced prey availability, with female condition and reproductive success reflecting ecosystem health (Christiansen *et al.*, 2018; Olivier *et al.*, 2022; Páez-Rosas *et al.*, 2021; Seyboth *et al.*, 2016; van den Berg *et al.*, 2021). Wide migrations and specialised foraging behaviours increase vulnerability to seasonal variations and changes in prey, habitat availability and anthropogenic stressors, including overfishing of prey, pollutants, and coastal developments (García-Baron *et al.*, 2019; Hays *et al.*, 2016; Sequeira *et al.*, 2018). Furthermore, wide-ranging pelagic species are vulnerable to bycatch and fishing induced mortalities, such as capture in long line fisheries (Báez *et al.*, 2019; Baker & Wise, 2005; Bentley *et al.*, 2021).

Generalist predators provide valuable insight into the health of marine ecosystems and several prey items across various trophic levels (Bertrand *et al.*, 2012; Hazen *et al.*, 2019; Thompson *et al.*, 2012; Velarde *et al.*, 2013). Spatio-temporal distributions of predators can be further used to inform conservation management and the state of fisheries (Chimienti *et al.*, 2017; Hays *et al.*, 2016; Santora *et al.*, 2017). Globally, the ocean is experiencing climate-induced shifts in habitat quality, primary productivity, and trophic cascades of prey availability; these shifts are reflected in both foraging site fidelity and habitat ranges in various marine predators (Louis *et al.*, 2021; Lukies, 2019; Wright *et al.*, 2017). Extreme and prolonged heatwaves negatively impact marine predators, with top-down and bottom-up stressors resulting in food scarcity and population decreases (Crawford *et al.*, 2022; Hanson *et al.*, 2021).

Flexible foragers can adapt to these anthropogenic and climate-induced changes, increasing foraging distance and duration due to food availability and distribution (Hückstädt *et al.*, 2020; Osborne *et al.*, 2020; Stephenson *et al.*, in review). Likewise, shifts in prey targeting reflect changes in low-level prey availability and interspecific interactions associated with habitat changes and ocean warming (Divoky *et al.*, 2021; Hamilton *et al.*, 2019; Watt *et al.*, 2016; Yurkowski *et al.*, 2017). While some species can switch prey, specialist feeders are vulnerable to collapsing fish stocks, particularly those targeted by

commercial fishers, with shifts in migration patterns reflecting preferred prey distribution and abundance (Johnson & Davoren, 2021; Szesciorka *et al.*, 2020). Spatial distribution of prey and predators can further be used to inform spatial management planning, with areas of rich primary productivity and prey availability reliably overlapping with marine hotspots (Armstrong *et al.*, 2021; Putra & Mustika, 2020; Rockwood *et al.*, 2020; Rohner *et al.*, 2020).

1.3.3 Ngā tohu o te Taio – Māori environmental indicators

Tohu are environmental indicators developed and used by Māori as resource management methods and marine protection in rohe moana (marine environment). Tohu indicate when and where to gather kaimoana (seafood) and measure the environment's health. Species-focused tohu, such as the availability, accessibility, and abundance of species, reflect the health of kaimoana and processes that affect ecosystem health. Process-focused tohu, such as multi-species foraging associations, reflect holistic views of the ocean and the condition and presence of processes that contribute to a healthy ecosystem (Philip *et al.*, 2012; Wilson *et al.*, 2007). Traditional knowledge of marine tohu provide valuable insights into ecosystem health, with shifts in population health and distribution reflecting the mauri (life force) of the species (Lyver *et al.*, 2008). For example, cultural harvest levels of sooty shearwaters (tītī; *Puffinus griseus*) reflect climate-related processes that impact prey distribution, abundance, and population health (Humphries & Möller, 2017; Moller & Thompson, 1999). Tohu can be used to collectively inform the overall wellbeing of mana whenua (Māori who have historic and territorial rights over the land) and health of the ecosystem (Tangaroa Tohu Mana, Tangaroa Tohu Mauri, marine cultural health programme: marineculturalhealth.co.nz). By combining mātauranga Māori and tohu with science, tikanga practices and sustainable management can better protect species and habitats showing signs of poor health.

1.4 The Hauraki Gulf - Tīkapa Moana - Te Moananui-ā-Toi

The Hauraki Gulf – Tīkapa Moana – Te Moananui-ā-Toi (hereafter referred to as the Gulf) is well recognised for its biological diversity, productivity, and the wide variety of marine ecosystems, including estuaries, rocky reef habitats and deep offshore environments it supports (Barbera, 2012; Chang *et al.*, 2003). Following human settlement, anthropogenic impacts and demands on the environment have exponentially increased, driving a loss of biodiversity and the destruction of marine habitats (Hamilton, 2020; Hauraki Gulf Forum, 2020; MacDiarmid *et al.*, 2016; Pinkerton *et al.*, 2012; Stephenson *et al.*, in review). A loss of natural vegetation, extensive land development, urbanisation, sedimentation have further reduced the health of marine environments in the Gulf (Gaskin & Rayner, 2013). Despite this, the Gulf region is a globally significant marine predator hotspot, with 20% of the world's seabird species (>70 species) and 25% of the world's whale and dolphin species having been seen in the productive waters (Hauraki Gulf Forum, 2020; Stephenson *et al.*, 2020).

Over 70 seabird species forage in the Gulf, showing a variety of foraging habits, with gulls, terns, cormorants, and penguins mainly feeding in tidal harbours and inshore waters, whereas petrels, shearwaters, and gannets forage pelagically in deeper waters offshore, including continental shelves (Gaskin & Rayner, 2013). The Gulf is a breeding ground for 27 seabird species, both resident and migratory, including petrels, shearwaters, cormorants, gulls, terns, the Australasian gannet (*Morus serrator*), and the little (blue) penguin (*Eudyptula minor*) (Gaskin & Rayner, 2013; Hauraki Gulf Forum, 2020; Whitehead *et al.*, 2019). Fourteen of these are endemic to New Zealand, meaning they don't breed anywhere else. Four of these are endemic to the Gulf: black petrel (*Procellaria parkinsoni*), Buller's shearwater (*Puffinus bulleri*), New Zealand fairy tern (*Sternula nereis davisae*) and Pycroft's petrel (*Pterodroma pycrofti*) (Gaskin & Rayner, 2013; Hauraki-Gulf-Forum, 2020).

In New Zealand, 41 recognised cetacean species have been identified, many of which have been sighted within the Gulf (Baker *et al.*, 2010; Stephenson *et al.*, 2020). The three most frequently sighted cetaceans in the Gulf include common dolphins (*Delphinus delphis*), Bryde's whales and bottlenose dolphins (*Tursiops truncatus*), all seen year-round (Dwyer *et al.*, 2016). There are also seasonal migrants, such as humpback whales (*Megaptera novaeangliae*), which pass through during their annual migration (Constantine *et al.*, 2007) and pygmy blue whales (*Balaenoptera musculus brevicauda*) (Olson *et al.*, 2015). False killer whales (*Pseudorca crassidens*), offshore bottlenose and long-finned pilot whales (*Globicephala melas edwardii*) are commonly found in the outer Gulf in summer-autumn feeding in deeper offshore waters (Zaeschmar *et al.*, 2013, 2014, 2020). In the Gulf's pelagic waters, mobulid rays (Duffy & Abbott, 2003; Setwayan, per comms.) and whale sharks (Duffy, 2002) are found foraging on plankton and small fish aggregations.

The gulf also supports a diverse array of predatory and piscivorous fish, including school (*Galeorhinus galeus*), bronze whaler (*Carcharhinus brachyurus*), and hammerhead sharks (*Sphyrna zygaena*), kahawai, skipjack tuna (*Katsuwonus pelamis*), kingfish (*Seriola lalandi lalandi*) and trevally; however, anthropogenic stressors have led to declines in population numbers of many of these species (Hauraki-Gulf-Forum, 2020). These declines are also observed in pinnipeds as a result of intensive hunting once people colonised the region, with commercial hunting reducing numbers to near-extinction (Hauraki-Gulf-Forum, 2020; MacDiarmid *et al.*, 2016; Pinkerton *et al.*, 2012). Although currently there are no seal or sea-lion colonies found within the gulf, recovery is evident with frequent sightings of fur seals (Department of Conservation, 2018, 2021).

1.5 Drones in ecology

The advancement of remote sensing tools has been transformative for ecological research, providing novel insights into fine-scale shifts in ecosystem health, furthering research, conservation, and education (Chen *et al.*, 2022; Reddy, 2021; Smith & Pinter-Wollman, 2021). The development of low-cost and easy to use unmanned aircraft systems (hereafter drones) by non-specialised operators is

revolutionising ecology, allowing surveys in challenging terrain to be more accessible and cost-efficient (Ivosevic *et al.*, 2015; Schaub *et al.*, 2018). These drones increase the spatial and temporal resolution of data, allowing researchers to independently collect high-quality visual data over multiple scales without resource-intensive aircraft or satellite-based imagery (Anderson & Gaston, 2013; Joyce *et al.*, 2018). Drone footage can be further used to validate and calibrate satellite imagery, allowing target features, such as habitat structures, to be easily detected (Bennett *et al.*, 2020). High-resolution data collection also increases sampling intensity and flexibility across narrow spatial ranges whilst supplementing on-board and on-ground observations in low-accessibility areas (Colefax *et al.*, 2018; Weimerskirch *et al.*, 2018). Equipping drones with remote-sensing instruments, including optical (infrared, ultraviolet and high-definition cameras), physical, chemical, and acoustic sensors, allows high-resolution imagery and ecological data to be collected at varying spatial and temporal scales (Gray *et al.*, 2018; Ivosevic *et al.*, 2015; Lyons *et al.*, 2019; Ventura *et al.*, 2018). Using drones minimises human survey effort while maximising spatial cover of surveys, enhancing data collection on cryptic species that spend significant time at sea or under the water (Seymour *et al.*, 2017).

However, the suitability of drones and aerial surveys to monitor species is limited by environmental variables, including glare, turbidity and wind speed, uniformity of background and crowding obstructing the field of vision (Benavides *et al.*, 2019; Colefax *et al.*, 2018; Dujon & Schofield, 2019). In behavioural ecology, the usability of drones is limited if there are behavioural and physiological responses to visual and auditory stimuli emitted from drones (Giles *et al.*, 2021; Vas *et al.*, 2015). For example, the species-specific disturbance, stress, and escape responses in birds (Borrelle & Fletcher, 2017; Weimerskirch *et al.*, 2018; Weston *et al.*, 2020), marine mammals (Castro *et al.*, 2021; Giles *et al.*, 2021; Ramos *et al.*, 2018) and pinnipeds (Laborie *et al.*, 2021; Rebolo-Ifrán *et al.*, 2019). While there are some concerns about the suitability of drones for ecology, developments of ethical guidelines and species-specific response studies enable researchers to minimise drone-induced disturbance and gain novel data and insights into aspects of their ecology that are difficult to observe and record using traditional research methods (Joyce *et al.*, 2018; Krause *et al.*, 2021; Oleksyn *et al.*, 2021; Vas *et al.*, 2015).

1.6 Artificial intelligence in ecology

Artificial intelligence (AI), also known as machine learning, uses annotated, non-linear data (such as audio and visual recordings) to 'teach' computers to identify, process and export readable data on various measurements, patterns, and features (Christin *et al.*, 2019; Gray *et al.*, 2019a). Using different AI models, such as Hidden-Markov and Gaussian mixture models (HMM and GMM's, respectively) and support vector machines, accurate detection and classification of objects or features in the data can be achieved at high sensitivities with low false discovery rates (Brown & Smaragdis, 2009; Ogundile *et al.*, 2021; Roch *et al.*, 2008). AI is a valuable tool for analysing and

classifying ecological data and performing various tasks, including automating the detection and classification of animals from photographs and audio recordings (Christin *et al.*, 2019; Nguyen *et al.*, 2017; Valletta *et al.*, 2017). Likewise, AI can track specific objects, features, and animals, classifying their movements and behaviours in labelled training data (Chalmers *et al.*, 2019; Olden *et al.*, 2008). AI removes inherent observer bias and errors when analysing lengthy and complex data sets (Christin *et al.*, 2019; Gray *et al.*, 2019a; Tabak *et al.*, 2019). AI tools have been used to process photographs (Kierdorf *et al.*, 2020), underwater digital images (Konovalov *et al.*, 2020), and drone footage (Gray *et al.*, 2019a; Gray *et al.*, 2019b) to differentiate cetaceans from their surroundings in photos and video frames, reducing manual processing time and enhancing workflows for researchers.

When analysing deep data, AI acts as a prediction tool rather than an analysis tool, extracting biologically or ecologically important information from complex data sets, which are typically limited by data analysis bottlenecks and manual processing time (Bicknell *et al.*, 2016; Seymour *et al.*, 2017; Valletta *et al.*, 2017). These tools can also be used to quickly describe and analyse acoustic recordings, photographs, and videos, providing rapid identification, translation, and analysis power for scientists (Chabot & Francis, 2016; Olden *et al.*, 2008). AI can extract pre-categorised ecological data across various spatial and temporal scales with minimal human input, enhancing the analysis of complex datasets (Dujon & Schofield, 2019; Goldstein *et al.*, 2019; Wang, 2019). AI often outperforms human observers, maximising flexibility, predictability, and responsiveness to shifts in data (Seymour *et al.*, 2017). AI can support the detection of visually cryptic, migratory, and mobile predators by increasing the capacity for analysing and translating large data sets generated by passive monitoring tools (Gibb *et al.*, 2019; Valletta *et al.*, 2017). AI is also a flexible approach to monitoring marine species, allowing data to be overlapped with known environmental variables and geographic information through multidisciplinary tools to better understand the drivers of observed data such as behaviours, abundance, and distribution (Ahmad, 2019).

While passive monitoring systems, such as drone technology, increase the temporal and spatial extent of survey efforts, large data sets are generated, highlighting the need for automated data processing (Dujon & Schofield, 2019; Tabak *et al.*, 2019). AI can simplify continuous and passive monitoring systems, such as hydrophones and drones, by automating time-consuming manual data extraction with minimal bias (Christin *et al.*, 2019; Dujon & Schofield, 2019). In soundscape research, AI can extract partial audio files containing items of interest from passive hydrophone recordings, such as whale calls, to minimise the duration of audio recordings manually sorted (Cuevas *et al.*, 2017). For example, cetacean vocalisations are detectable using discrete spectral compositions, allowing for rapid detection and classification of species present (Brown & Smaragdis, 2009; Cuevas *et al.*, 2017; Roch *et al.*, 2008).

AI has also been developed to aid citizen science projects. For example, image recognition tools enable the automatic detection and tracking of cetaceans using fluke and fin scarring, and body colouration patterns as digital fingerprints (<https://www.flukebook.org>). Likewise, by combining AI and citizen science, fixed camera footage can be processed using citizen trained imagery, producing meaningful metrics on penguin colonies' abundance and spatial structure (<https://www.zooniverse.org>; Penguin watch) (Arteta *et al.*, 2016; F. Jones *et al.*, 2018, 2020). Crowdsourced databases enable rapid and accurate identification of individuals across populations by sharing tedious and time-consuming AI training tasks (Blount *et al.*, 2019). By combining these multidisciplinary toolsets, scientists can better utilise machine learning and AI tools to answer complex ecological questions and address time-sensitive ecosystem stressors and threats.

1.7 Thesis Structure

The main aim of this research is to investigate MSFA dynamics in the Gulf. Using both the University of Auckland research vessel *RV Hawere* and Auckland Whale and Dolphin Safari vessel *MV Dolphin Explorer*, we examine the seasonal dynamics and MSFA communities present within the Gulf. In addition, this research will aim to determine whether machine learning and drone technology is a viable tool for furthering our ability to analyse MSFA dynamics. This thesis comprises three research chapters (Chapters 2 to 4) with a general introduction and general discussion (Chapters 1 and 5, respectively). Chapter 2 aims to use attendance patterns to characterise MSFA dynamics and characterise MSFAs by clusters of attendees. Chapter 3, however, takes a behavioural ecology approach, using activity budget analysis to provide an overview of group foraging behaviours within MSFA events in relation to seasons and MSFA composition. To conclude this research, chapter 4 investigates the use of multi-disciplinary tools to further our understanding of MSFA dynamics by developing a proof-of-concept machine learning tool to analyse drone footage.

Chapter 1 - General Introduction

This chapter introduces the study and presents an overview of the literature on the drivers behind MSFA formation. We describe cues that marine animals, primarily seabirds and cetaceans, use to detect ephemeral and patchily distributed prey and the fine-scale foraging behaviours of these animals. This review also explores the use of drones and AI in behavioural ecology and wildlife conservation.

Chapter 2 - MSFA Dynamics and Composition

Chapter 2 assesses the predator species composition of MSFAs through demographic analyses, including investigating presence and absence patterns, distinguishing MSFA communities, and identifying social affinity indexes for species pairs. We discuss these findings in relation to seasonal movement patterns, prey specificity and known foraging ecologies. Furthermore, we highlight the

need for further studies to expand survey efforts to capture near-shore and off-shore pelagic MSFA events.

Chapter 3 - MSFA Activity Budgets

Here we compare activity budgets between and within species through the proportion of time groups spent foraging, active non-foraging, and non-active non-foraging within MSFA events. Using activity budgets, we provide an insight into the proportion of time species spend in various behavioural states in relation to MSFA composition and season.

Chapter 4 - Multidisciplinary tools to investigate MSFAs

Here we develop a proof-of-concept AI tool to detect and classify seabird and cetacean presence and their behaviours from drone imagery of MSFA events and individual species groups. Incorporating AI-assisted tagging and drone imagery is a powerful and accurate monitoring tool, reducing manual processing time and increasing the capacity of researchers to detect fine-scale behaviours and patterns of associations and community composition.

Chapter 5 - Summary synopsis

In this final chapter, we tie together the overall findings of this thesis with a synopsis serving as a summary of this research. Through this synthesis, we identify key areas which require further study and suggest directions for future studies.

Chapter 2 MSFA Dynamics and Composition

2.1 Introduction

Marine MSFAs are dynamic ocean events driven by predators whereby two or more species forage on the same ephemeral prey patch (Clua & Grosvalet, 2001; Gostischa *et al.*, 2021). MSFAs develop through positive (facilitation and mutualism) and negative (competition and predation) species interactions, with community composition reflecting the trade-offs and benefits of foraging alongside hetero- and conspecifics (Bulleri *et al.*, 2016; Stachowicz, 2001; Veit & Harrison, 2017). Facilitative relationships that form between species foraging in MSFAs can extend foraging niches through reduced anti-predator vigilance, and increased prey detection and accessibility for joining species (Cresswell *et al.*, 2003; Goyert *et al.*, 2014; Goyert *et al.*, 2018a; Sridhar *et al.*, 2009). However, the availability and abundance of prey determine the benefits of, and foraging behaviours used within MSFAs (Benoit-Bird *et al.*, 2013; Boyd *et al.*, 2015; Cansse *et al.*, 2020; Gostischa *et al.*, 2021). Both intra- and inter-specific competition result in particular foraging behaviours and strategies, allowing species to exploit ephemeral and patchily distributed prey patches, and coexist due to niche separation and asymmetrical responses to cues (Goodale & Nieh, 2012; Hamilton, 2020; Svanbäck & Bolnick, 2007).

In the marine environment, these aggregations involve multiple species, including but not limited to marine mammals (Au & Pitman, 1986; Montero-Quintana *et al.*, 2021; Vaughn *et al.*, 2007, 2008), seabirds (Maynard & Davoren, 2020) and large predatory fish, including sharks and tuna (Clua & Grosvalet, 2001; Sutton *et al.*, 2020). MSFAs often involve aerial and subsurface predators, with prey detection and aggregations resulting in facilitated foraging opportunities (Au & Pitman, 1986; Clua & Grosvalet, 2001; Miller *et al.*, 2018; Tremblay *et al.*, 2014). Subsurface herding behaviours counteract the vertical scattering effect of diving seabirds, forcing prey to the surface, and enhancing foraging success for surface foragers through highly coordinated herding behaviours within and between species (Benoit-Bird & Au, 2009; Gatti *et al.*, 2021; McInnes & Pistorius, 2019; Vaughn *et al.*, 2010; Vaughn *et al.*, 2008). Pursuit-plunging and pursuit-diving seabirds exert vertical scattering effects on prey, reducing the foraging efficiency of depth-limited, non-diving seabirds (Hoffman *et al.*, 1981; Hulsman & Tularam, 2021). Scavenging seabirds feed alongside predators, contributing little to the maintenance of flocks (Chilton & Sealy, 1987; Pitman & Ballance, 1992). Scattering effects are evident in large surface feeding predators. For example, baleen whales often forage alongside other marine predators, both planktivores and fish-eating, lunge feeding at the centre of MSFA events, terminating the feeding event through consuming large proportions of prey (Gostischa *et al.*, 2021; Haynes *et al.*, 2011; Hoffman *et al.*, 1981).

MSFA events are facilitated through hierarchical mechanisms (Stukalyuk & Radchenko, 2011), foraging opportunities (Anderwald *et al.*, 2012; McInnes & Pistorius, 2019; Miller *et al.*, 2018), information transfer (Cook *et al.*, 2017; Falcón-Cortés *et al.*, 2019) and multi-layered social networks (Meise *et al.*, 2020). MSFA composition can provide information on the species interactions, with highly skilled foragers enhancing foraging opportunities for others (Clua & Grosvalet, 2001; Gostischa, 2020) and subordinates experiencing more benefits than dominant species (Hino, 2000). Reaction distances and attendance to MSFAs is both species- and context-specific, with social information, such as the species present and aggregation distance, influencing the likelihood of joining MSFA events (Purvin, 2015; Sridhar *et al.*, 2009; Thiebault *et al.*, 2014). Nuclear species that initiate MSFA events tend to be in larger numbers than following subordinates, highlighting that dominant and gregarious species attract other species' attention, leading to the formation of MSFA events (Goodale & Beauchamp, 2010; Srinivasan *et al.*, 2018). MSFA attendance and benefits received by individuals is influenced by competition avoidance (Ronconi & Burger, 2011), predator-prey relationships and foraging ecologies (Au & Pitman, 1986; Ballance *et al.*, 1997; Pitman & Ballance, 1992; Vaughn *et al.*, 2007). For species to attend MSFAs, the benefits of foraging in close association must outweigh the perceived and actual costs (Evans, 1982; Hirsch, 2007; Sridhar & Shanker, 2014; Stensland *et al.*, 2003). While some species may benefit from increased accessibility to prey, others may face increased predation or injury risk, leading them to avoid MSFAs containing certain species, such as kleptoparasites and predators (Lukoschek & McCormick, 2000; Machovsky-Capuska *et al.*, 2011a; Stensland *et al.*, 2003). Predation risk may be mitigated by exploiting the vigilance of others, reducing their own vigilance, in turn increasing their foraging efficiency (Cresswell *et al.*, 2003; Sridhar *et al.*, 2009). Social contexts and predator-prey relationships are important structuring forces that determine MSFA composition and species co-occurrence patterns (Sridhar *et al.*, 2013; Srinivasan *et al.*, 2010; van Opzeeland *et al.*, 2005).

MSFA dynamics are indicative of responses to seasonal and anthropogenically driven shifts in habitat and prey quality, with MSFA attendees acting as valuable indicators of prey availability, ecologically important areas and ecosystem health (Cox *et al.*, 2018; Gostischa *et al.*, 2021; Santora *et al.*, 2012; van Opzeeland *et al.*, 2005). Shifts in foraging association patterns may provide a more complete, holistic understanding of predator associations, with current association patterns acting as a baseline for understanding species dynamics under future ecosystem changes (Gulka *et al.*, 2017; Santos *et al.*, 2018; Veit & Harrison, 2017).

This chapter aims to identify MSFA dynamics by determining the presence and absence of species of marine predators within MSFA events in the Hauraki Gulf. In doing so, we will analyse patterns of attendance to identify key clusters and communities of species and investigate the potential drivers of these association patterns. Using presence-absence patterns, we aim to determine the social affinity index between species pairs to understand MSFA dynamics and species interactions better.

2.2 Methodology

2.1.1 Study Location

This study was carried out in the Hauraki Gulf – Tīkapa Moana – Te Moanaui-ā-Toi (hereafter referred to as the Gulf) on the north-eastern coast of the North Island – Te Ika a Māui, Aotearoa New Zealand. This region extends between 36° 10' to 37° 10' S and 174° 40' to 175° 30' E (Figure 2.1). The region is oceanographically diverse, with volcanic islands, upwelling zones, shipping channels and shallow embayments with depths of 50-60m in the inner and central gulf to 50-100m in the outer Gulf (Manighetti & Carter, 1999). Oceanographic circulation and productivity within the Gulf are driven by surface winds, tidal currents, and physical barriers, such as islands and headlands (Black *et al.*, 2000).

The Gulf is a productive ecosystem and hotspot for marine predators, such as seabirds and cetaceans (Berkenbusch *et al.*, 2013; Gaskin & Rayner, 2013; Hauraki-Gulf-Forum, 2020; Stephenson *et al.*, 2020). Sea surface temperature ranges between 21°C in summer and 14°C in winter due to upwelling and warm currents (Hurst *et al.*, 2012). The Gulf experiences influxes of warm water from the East Auckland Current, an offshoot of the East Australian Current, and the upwelling of cool, nutrient-rich waters, making it a productive ecosystem (Zeldis *et al.*, 2004).

2.1.2 Data collection

Fieldwork was conducted from September 2019 to August 2021 onboard the University of Auckland's 15m research vessel, the *RV Hawere*, and the 20m Auckland Whale and Dolphin Safari (AWADS) vessel, the *MV Dolphin Explorer*. Fieldwork was conducted two to three days per month with vessel routes dependent on prevailing weather conditions, time to find feeding aggregations and prior knowledge of MSFA event locations to maximise encounter rates. When sea conditions deteriorated (Beaufort >3, wind >20 knots), the vessel returned to shore. The vessel tracks were continuously recorded using vessel tracking software, logging GPS coordinates during surveys. Three to six observers used binoculars and the naked eye, employing continuous scanning methodology to detect signs of MSFA activity, including whale blow, surface disturbance and flying or diving seabirds. MSFA events were defined as aggregations of two or more species foraging in a coordinated manner (Clua & Grosvalet, 2001). Each MSFA event was recorded individually and included only the species observed during that event and included all potentially interacting individuals within the feeding area.

Surveys on *RV Hawere* were dedicated MSFA survey trips averaging 6.5 hours; however, those on *MV Dolphin Explorer* were commercial whale-watch trips which were approximately 4.5 hours long. *MV Dolphin Explorer* surveys tended to target MSFA events involving marine mammals; when seabird-only MSFA events were detected, the vessel did not stop. Conversely, seabird only MSFA event participants and behavioural observations were recorded to the best of our ability with the

assistance of binoculars. Irrespective of the research platform, for each MSFA event, we recorded GPS locations, the number of animals, species present, behaviours and prey type (if observed). MSFAs were observed until feeding activity stopped, time constraints forced the vessel to move on, or a representative sample of the MSFA event had been recorded.

2.2.3 Data analysis

All analyses were conducted in R-studio (Version 1.4.1717), Primer-e (Version 7 + PERMANOVA) and SOCPROG (Version 2.9). Within RStudio, the 'tidyr' package (Wickham, 2021) was used for data management and reorganisation and 'ggplot' (Wickham, 2016) and "igraph" (Csardi & Nepusz, 2006) packages for data visualisation. To simplify the data, due to their low attendance rates, unidentified, fairy (*Sternula nereis*) and Caspian terns (*Hydroprogne caspia*) were combined to form 'unidentified terns'. Likewise, due to their functional and ecological similarity, white-faced storm petrels (*Pelagodroma marina*) and New Zealand storm petrels (*Fregetta maoriana*) were combined to form the group 'storm petrels' (Marchant & Higgins, 1990; Warham, 1990, 1996).

Attendance

To quantify the attendance of species within MSFA events, we calculated attendance as the percentage of workups in which each species and species group was encountered. Attendance ranged from 0% (never attending) to 100% (always attending). To investigate patterns of attendance, the mean group size of species was compared using a generalised linear mixed model (GLM) with a quasi-poisson error distribution. Using GLM's, we tested the effects of type of species (n = 22), cluster (n = 8), season (n = 4) and MSFA richness (number of species) on mean group size. GLM results were then investigated using a one-way analysis of variance (ANOVA) and pair-wise comparison for factor levels.

Community composition

The Margalef species richness index (d, Equation 2.1) and Shannon-Weiner diversity index (H' , Equation 2.2) were calculated for each MSFA event to indicate the total number of species within an MSFA and species evenness and dominance within a community.

Equation 2.1 Margalef's Richness Index

$$d = \frac{S - 1}{\text{Log}(N)}$$

Equation 2.2 Shannon-Weiner Diversity Index

$$H' = - \sum_{i=1}^S (p_i \ln p_i)$$

S is the total number of species; *N* is the total number of individuals.

Using PRIMER-E, a Bray-Curtis similarity index (S) (hereafter 'Bray-Curtis Similarity') was generated, allowing us to determine variables that influence the observed community structure (Clarke & Ainsworth, 1993; Clarke & Warwick, 2001). This index was used to quantify the similarity (or "distance") between two MSFAs, representing the similarity between the j^{th} and k^{th} samples, with y_{ij} representing the abundance of the i^{th} species in the j^{th} MSFA. Similarly, y_{ik} is the count for the i^{th} species in the k^{th} sample. The index is bounded between 0 and 1, with one completely similar and zero entirely different.

$$S_{jk} = 100 \left\{ 1 - \frac{\sum_{i=1}^p |y_{ij} - y_{ik}|}{\sum_{i=1}^p (y_{ij} + y_{ik})} \right\}$$

Abundance data were square-root transformed to reduce the dominant contribution of abundant species. Non-metric multidimensional scaling and a hierarchical cluster analysis were conducted with Primer-7 to determine community types (hereafter clusters). The generated Pearson matrix correlation (r , cophenetic correlation) explains how accurately the dendrogram represents the relationships between MSFAs, with r -value of 1 indicating excellent representation. SIMPER (similarity pair-wise comparison ANOSIM test) analysis was performed, clustering MSFAs into compositionally similar clusters and identifying species and their relative contribution to observed differences between MSFAs. ANOSIM analysis compares similarities between MSFAs. R values close to 1 suggest MSFAs are different, while R values close to 0 indicate an even distribution. MSFA composition was further tested using a non-parametric permutational multivariate analysis of variance (PERMANOVA), which can analyse interactions between factors.

Social Affinity Index

Social affinity and network analysis describes the interactions and/or associations between individuals, groups, and species in a population (Whitehead, 1997, 2018). Social affinity analysis was conducted in SOCPROG v2.9 using square root transformed data of presence and absence of species (Whitehead, 2009). Values for social affinity were calculated using the simple ratio method, using the co-occurrence of species to determine the degree of affinity (with values towards 1 indicating always co-occurring and 0 never) between species pairs. Values above 0.3 provide evidence of frequent co-occurrence and structure within species pairs (Whitehead, 2019). Using SOCPROG, permutations ($n = 1000$) were used to test for non-random associations and preferred associations, with calculated p values providing confidence in the accuracy of these identified species pairings and thus indicating social affinity. These indices were combined with the number of associating species (degrees) to generate a social affinity matrix and matrix plot using "igraph".

2.3 Results

Attendance

Between September 2019 and August 2021, we collected data on 179 MSFA events from 45 trips and 198 hours of survey effort (time vessel left the wharf until its return). Twenty trips were undertaken on *RV Hawere* and 24 trips on *MV Dolphin Explorer*, with an average survey duration of 5.2 hours and 3.4 hours respectively. Survey effort was undertaken in the Gulf, with MSFA events recorded from Great Barrier Island (Aotea) to the east coast of the Coromandel peninsula, with *RV Hawere* and *MV Dolphin Explorer* departing from Ti Point wharf and the Viaduct Basin, respectively (Figure 2.1).

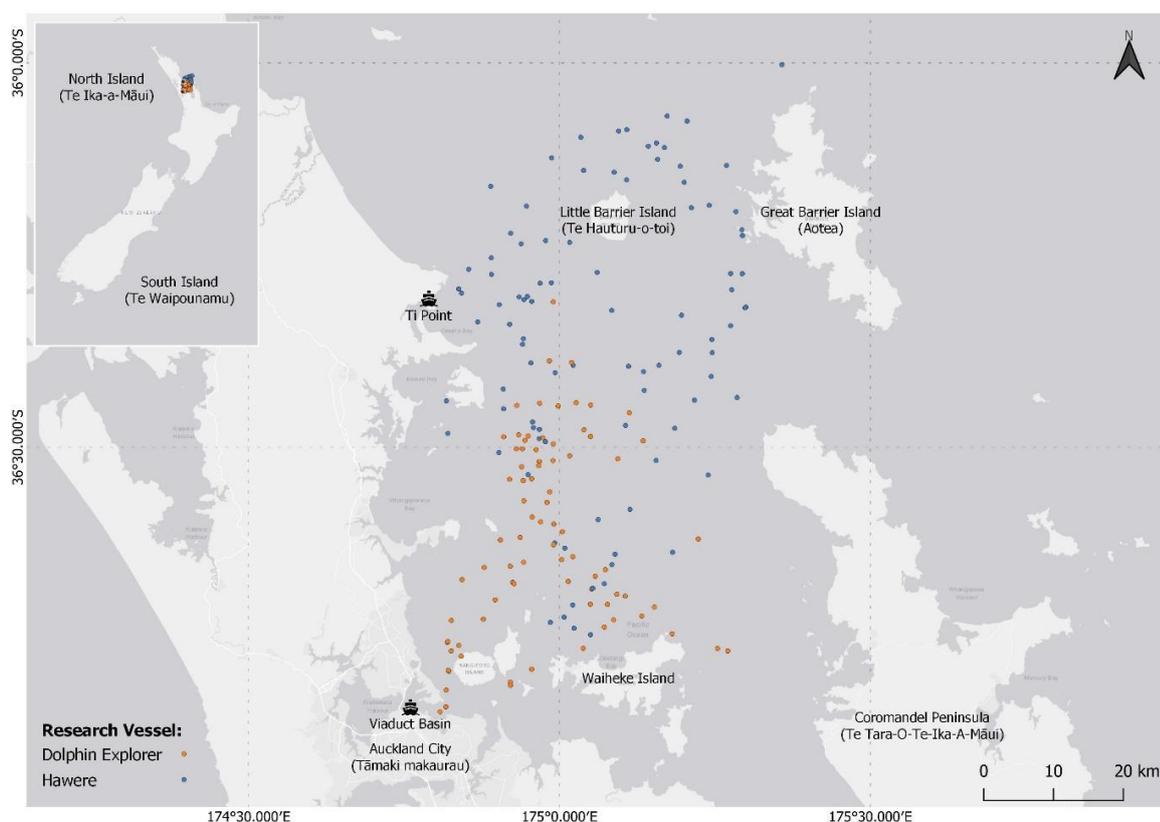


Figure 2.1 Map of research area with MSFA events (•, n = 179) and departure locations (Ti Point and Viaduct Basin) labelled.

Over 179 MSFA events, we recorded 33,843 individuals belonging to 22 species groupings: 16 seabird species, three cetacean species and three genus level seabird groups (unidentified terns, unidentified petrel/shearwater, and storm petrels). Of these MSFA events, 33% (n = 59) were seabird only and 67% (n = 120) involved both seabirds and cetaceans. MSFA event attendance (Table 2.1) ranged from two to 120 MSFAs attended, with the most frequently attending species being Australasian gannets (n = 120), common dolphins (n = 98), and fluttering shearwaters (n = 111). MSFA events were variable, with a mean of 3.7 ± 0.1 SE species and 158.6 ± 17.8 SE individuals

attending, although MSFA size and richness was variable across events (range: 2 - 1936 individuals and 2 - 8 species, respectively).

Table 2.1 Summary statistics of species attendance within MSFA events (n = 179).

Name		MSFAs Attended			Group Size		
Common Name	Species Name	Alpha Code	Total	%	Mean	Median	Range
Buller's shearwater	<i>Ardenna bulleri</i>	ARDBUL	43	24	37	10	1-500
Flesh-footed shearwater	<i>Ardenna carneipes</i>	ARDCAR	71	39.7	18	10	1-130
Sooty shearwater	<i>Ardenna griseus</i>	ARDGRI	7	3.91	4	3	2-10
Bryde's whale	<i>Balaenoptera edenei brydei</i>	BALBRY	43	24	1	1	1-6
Common dolphin	<i>Delphinus delphis</i>	DELDEL	98	54.7	70	37.5	4-500
Little penguin	<i>Eudyptula minor</i>	EUDMIN	7	3.91	2	2	1-3
Black-backed gull	<i>Larus dominicanus</i>	LARDOM	31	17.3	3	1	1-15
Red-billed gull	<i>Larus novaehollandiae</i>	LARNOV	14	7.82	4	2	1-20
Giant petrel	<i>Macronectes halli</i>	MACHAL	4	2.23	2	1.5	1-5
Australasian gannet	<i>Morus serrator</i>	MORSER	120	67	77	50	1-600
Fairy prion	<i>Pachyptila turtur</i>	PACTUR	2	1.12	25	25	10-40
Diving petrel	<i>Pelecanoides urinatrix</i>	PELURI	11	6.15	6	3	1-20
Pied shag	<i>Phalacrocorax varius</i>	PHAVAR	7	3.91	4	1	1-20
Black petrel	<i>Procellaria parkinsoni</i>	PROPAR	4	2.23	43	35	3-100
Cook's petrel	<i>Pterodroma cookii</i>	PTECOO	7	3.91	6	5	1-20
Grey-faced petrel	<i>Pterodroma gouldi</i>	PTEGOU	6	3.35	16	7.5	1-50
Fluttering shearwater	<i>Puffinus gavia</i>	PUFGAV	111	62	97	32.5	1-2000
White-fronted tern	<i>Sterna striata</i>	STESTR	44	24.6	63	30	1-600
NZ storm petrel	<i>Fregetta maoriana</i>	STOPET	25	14	14	5	1-100
White-faced storm petrel	<i>Pelagodroma marina</i>						
Bottlenose dolphin	<i>Tursiops truncatus</i>	TURTRU	2	1.12	8	8	6-10
Unid. shearwater/petrel	-	UNIDPE	1	0.56	5	5	5
Unid. tern	-	UNIDTE	8	4.47	9	2.5	1-30

Cluster Analysis:

Using the 179 MSFA events, data were transformed into a matrix of species presence-absence data (1 if present, 0 if absent), and hierarchical clustering (Bray-Curtis similarity index) was performed, identifying eight unique clusters. Hierarchical clustering dendrogram from Bray-Curtis similarity produced well-defined clusters with significantly ($p = 0.05$) distinct MSFA communities based on SIMPROF analysis. At each successive step of clustering, the two clusters with the greatest similarity are linked together. The horizontal axis indicates separation and dissimilarity between MSFA composition and the vertical axis, indicating the level of similarity between MSFA events (Figure 2.2a).

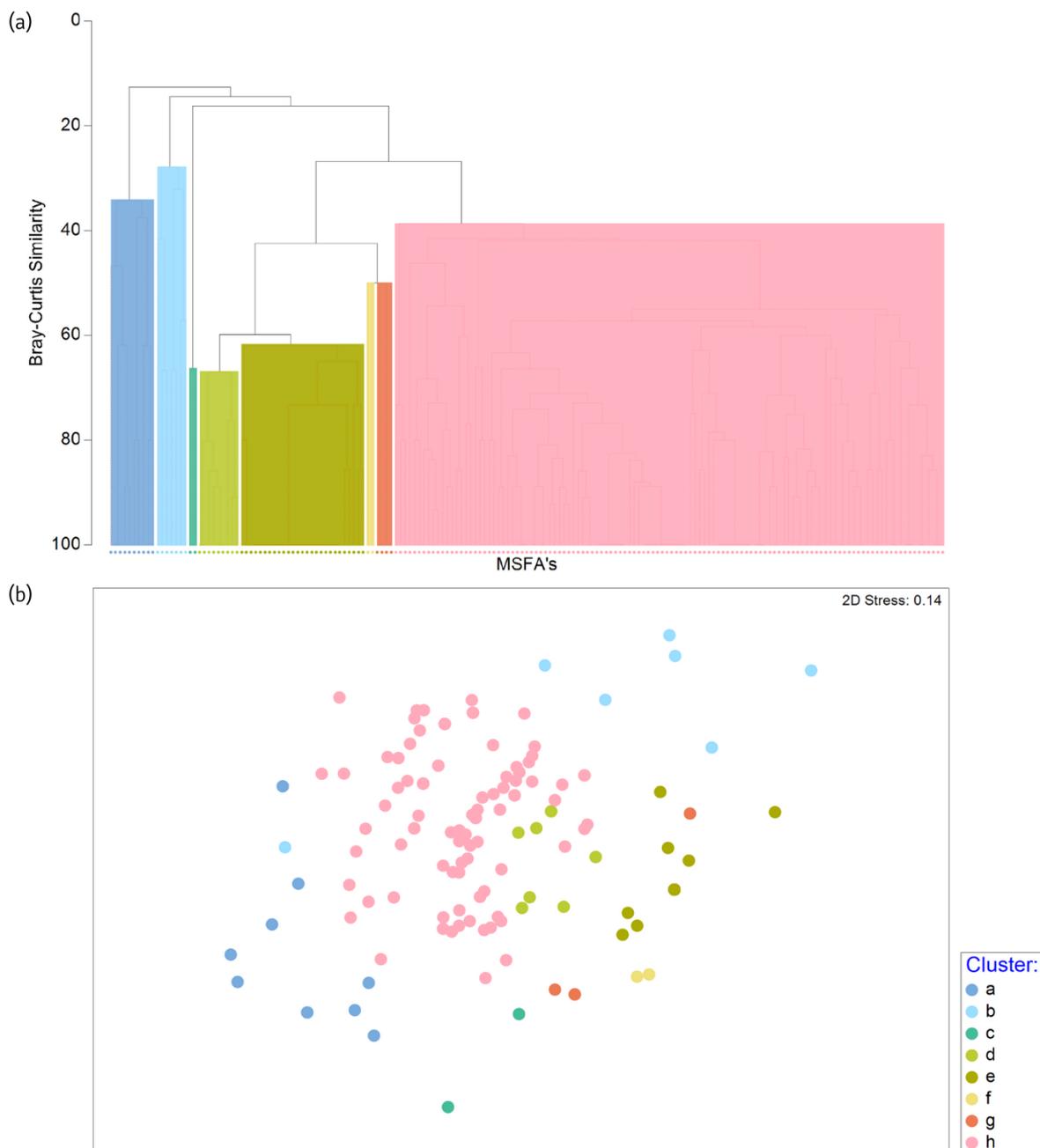


Figure 2.2 (a) Hierarchical clustering dendrogram and (b) non-metric MDS ordination of Bray-Curtis similarity of 179 presence-absence transformed MSFAs with SIMPROF one-way analysis overlaid.

Of the eight MSFA clusters identified (Figure 2.2), Cluster h was the most frequently recorded, accounting for 66% (n = 118) of the 179 MSFA events. Cluster e was observed on 15% (n = 27) of the events and all others were observed on ten or fewer occasions. Similarity percentage analysis (SIMPER, Table 2.2) identified ten species accounting for differences between MSFAs. Clusters a, e, f and g represent predominantly plankton-feeding (hereafter planktivorous) aggregations, with a predominance of planktivorous predators including Bryde’s whales, storm petrels, fluttering shearwaters, and white-fronted terns. Cluster b reflects scavenging opportunities, with the MSFAs dominated by scavenging seabirds. Cluster c is indicative of fish-based aggregations. Cluster d and h are indicative of multi-trophic aggregations (hereafter piscivorous) due to the cumulative contribution of piscivorous common dolphins and Australasian and planktivorous fluttering shearwaters.

Table 2.2 SIMPER analysis of the contribution of each species (%) to the similarity between MSFAs calculated from the Bray-Curtis Similarity index.

Cluster	Similarity	Species	Average presence	%	Cumulative %
a	44.26	Bryde’s whale	0.9	63.66	63.66
		Storm petrels	0.5	16.55	80.21
b	35.10	Black-backed gull	0.86	62.37	62.37
		Red-billed gull	0.43	75.94	75.94
c	66.67	Buller’s shearwater	1	50	50
		Fairy prion	1	50	100
d	75.81	Australasian gannet	1	30.32	30.32
		Fluttering shearwater	1	30.32	60.64
		White-fronted tern	1	30.32	90.96
e	84.67	Fluttering shearwater	0.96	49.52	49.52
		White-fronted tern	0.96	49.52	99.04
f	58.33	Fluttering shearwater	1	85.71	100
g	50	Fluttering shearwater	1	100	85.71
h	55.44	Australasian gannet	0.92	38.92	38.92
		Common dolphin	0.78	28.89	67.78
		Fluttering shearwater	0.58	13.70	81.47

Season Analysis:

When examining whether there were temporal changes in MSFA attendance, we used MSFA attendance to investigate the effects of seasonal movements and prey shifting on MSFA community dynamics. The 179 MSFA events were evenly distributed across summer (n = 44), autumn, (n = 36), winter (n = 52) and spring (n = 47). Species attendance (number of MSFA's attended) across these seasons varied, reflecting movement patterns, and changing prey availability in the Gulf (Figure 2.3).

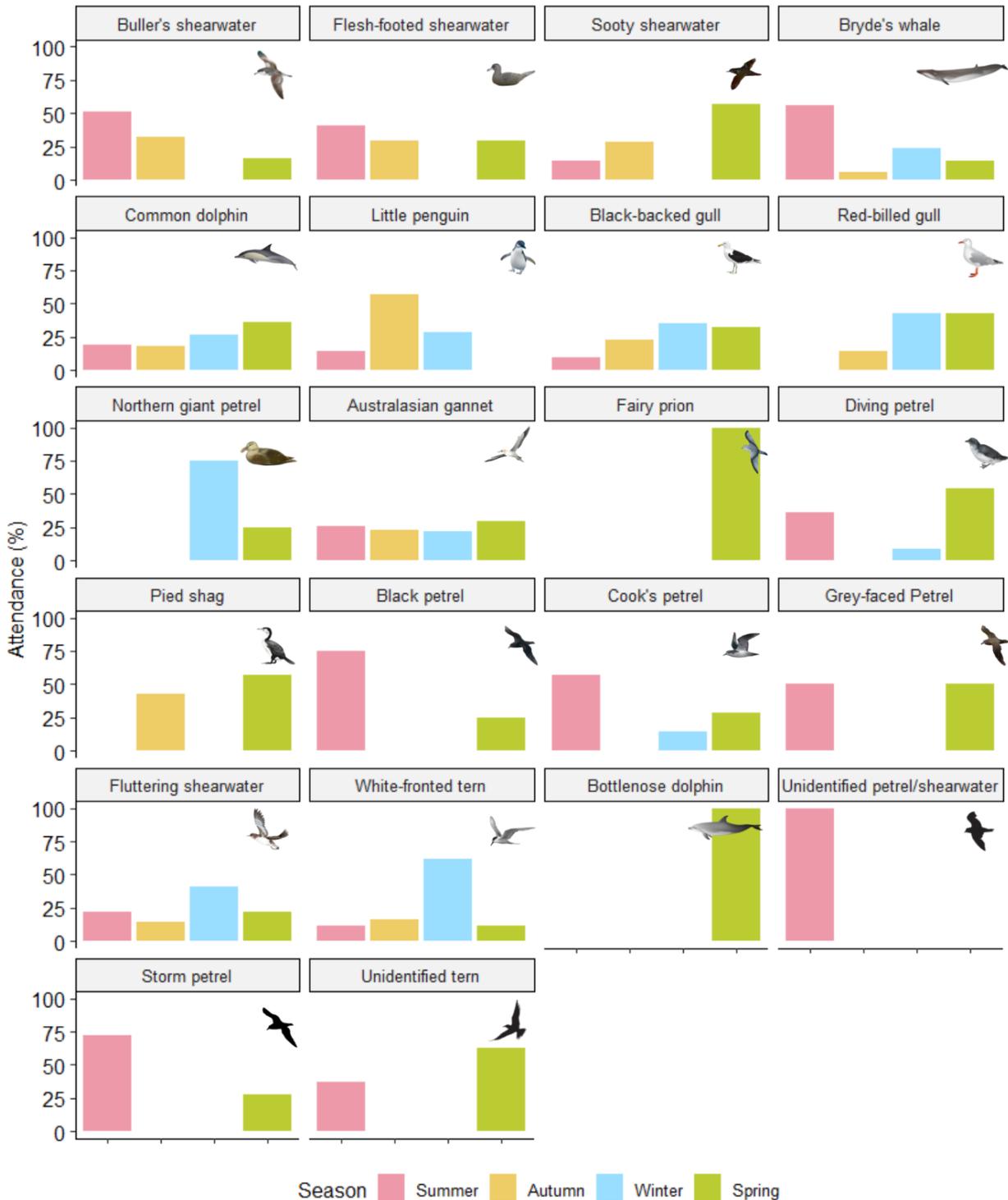


Figure 2.3 MSFA attendance patterns (% of sightings) across seasons, by species (n = 22).

The frequency of cluster occurrence across the seasons further reflects variation in preferred prey availability or migration of species that characterise clusters. Some clusters (e.g., cluster c) were exclusively found in one season, whereas multi-trophic MSFA events (cluster d and h) were found across all seasons (Figure 2.4).

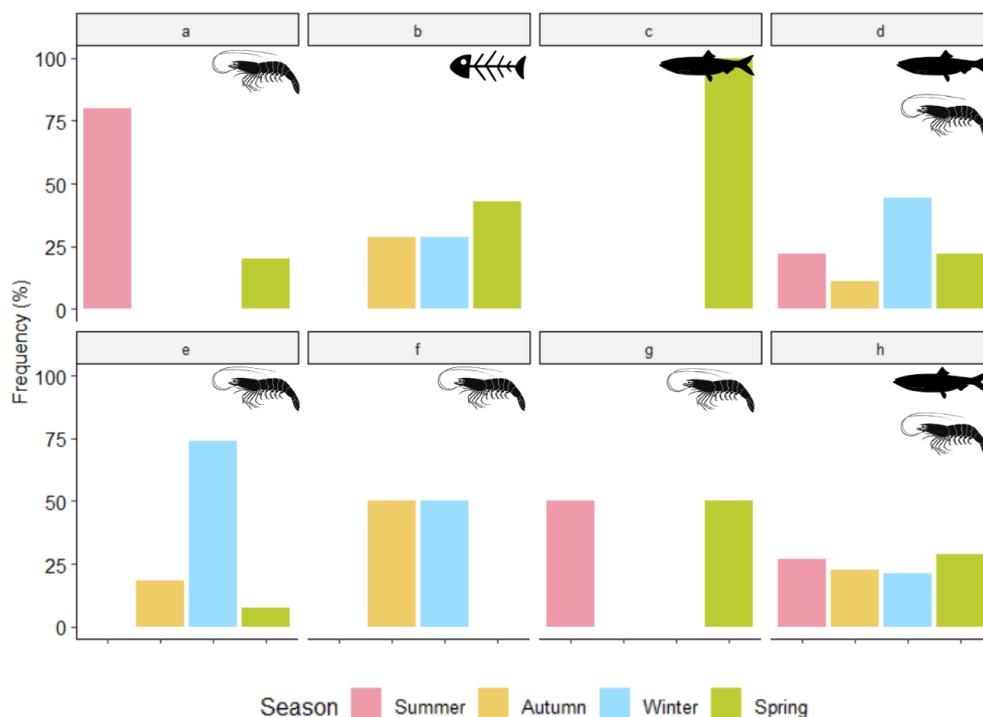


Figure 2.4 Frequency of cluster occurrence (%) by season. Icons represent diets of predominant species within-cluster: planktivores (icon: krill), scavengers (icon: fish skeleton), and piscivores (icon: fish).

Species attendance across these clusters varied, reflecting prey availability and preferred associations (Figure 2.4). The SIMPER analysis reflects these attendance patterns, with those with high percentage of cluster events attended highlighting their contribution to the characterisation of those clusters (Table 2.2). Using known diets, species presence in an MSFA can be an indication of the type of prey present, with attendance suggesting the availability of sufficient preferred prey.

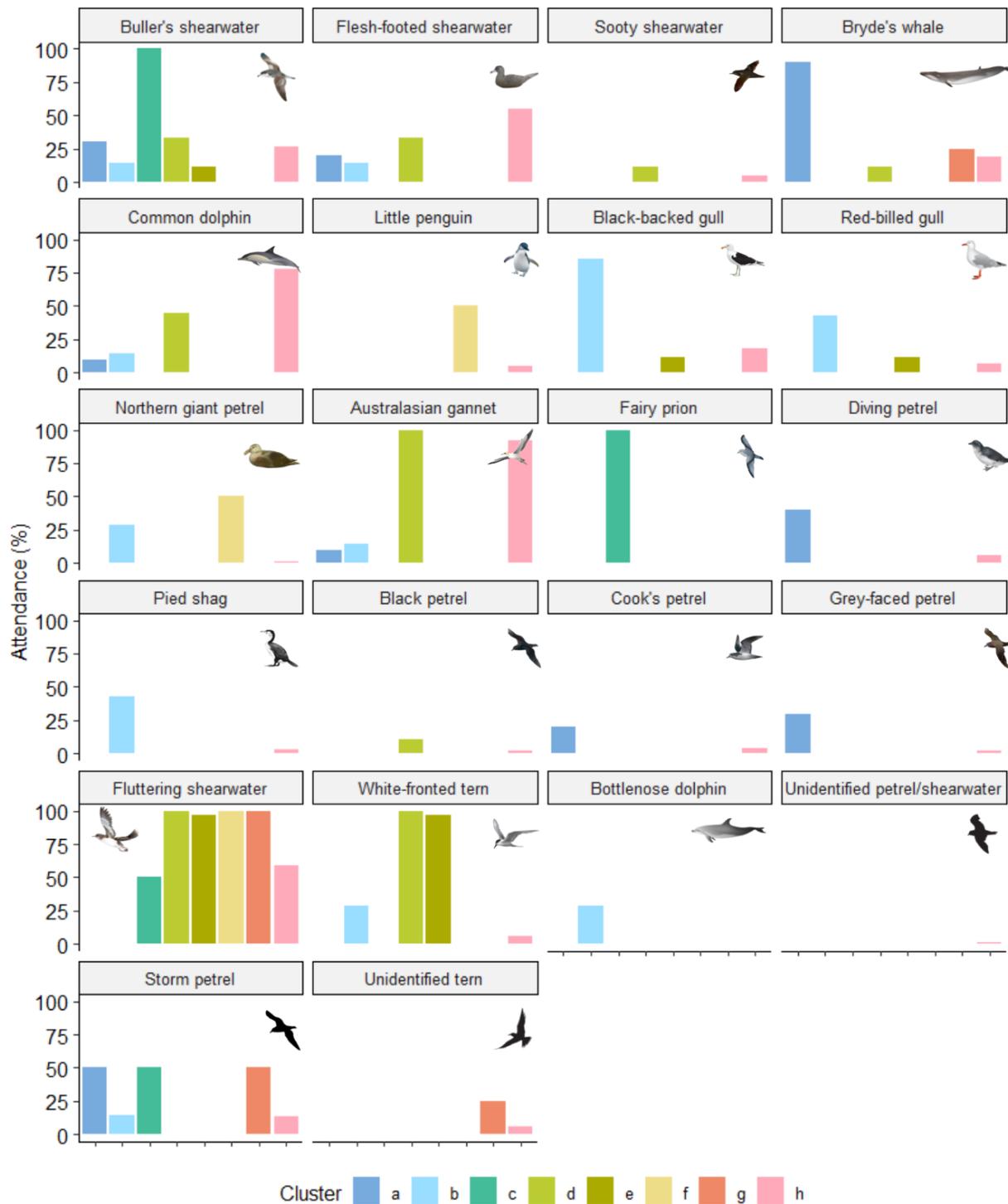


Figure 2.5 MSFA attendance patterns across clusters (a – h), by species (n = 22).

Group size:

Group size was found to vary by species, cluster, season, Shannon-Weiner diversity and Margalef's richness index (GLM, ANOVA, $p < 0.005$). Group size (estimate \pm SE) decreased with diversity (-1.69 ± 0.21) and increased (0.97 ± 0.25) with richness ($p < 0.005$). Pairwise comparison revealed that group sizes were smaller in autumn than winter (estimate \pm SE; -0.55 ± 0.18 ; $p = 0.01$) and spring than winter (estimate \pm SE; -0.7 ± 0.18 ; $p = 0.01$). All other season pairs were insignificant ($p > 0.05$).

Association index

Here, we examine foraging associations in more detail by considering species co-occurrence patterns and simple index ratios within MSFAs. Association indexes of zero were removed for this analysis. Using association indexes (Appendix 1), 131 pairs of species were identified with a mean \pm SE association index of 0.17 ± 0.014 . However, these indexes ranged from 0.03 - 0.9, with low indexes indicating low co-occurrence within MSFAs and indexes closest to 1 indicating frequent co-occurrence within MSFAs. The number of species they are seen co-occurring with during MSFA events (degrees, Table 2.3) ranges from 19 (Australasian gannets and flesh-footed shearwaters) to three (bottlenose dolphins) with a mean of 11.91 degrees ± 1.13 SE.

Table 2.3 The number (degrees) of species co-occurring (associations) during MSFA events.

Species name	Species code	Degrees
Buller's shearwater	ARDBUL	18
Flesh-footed shearwater	ARDCAR	18
Sooty shearwater	ARDGRI	8
Bryde's whale	BALBRY	18
Common dolphin	DELDEL	18
Blue penguin	EUDMIN	7
Black-backed gull	LARDOM	17
Red-billed gull	LARNOV	13
Giant petrel	MACHAL	9
Australasian gannet	MORSER	19
Fairy prion	PACTUR	3
Common diving petrel	PELURI	10
Pied shag	PHAVAR	10
Black petrel	PROPAR	9
Cook's petrel	PTECOO	8
Grey-faced petrel	PTEGOU	10
Fluttering shearwater	PUFGAV	19
White-fronted tern	STESTR	13
Storm petrel	STOPET	14
Bottlenose dolphin	TURTRU	3
Unidentified shearwater or petrel	UNIDPE	4
Unidentified tern	UNIDTE	14

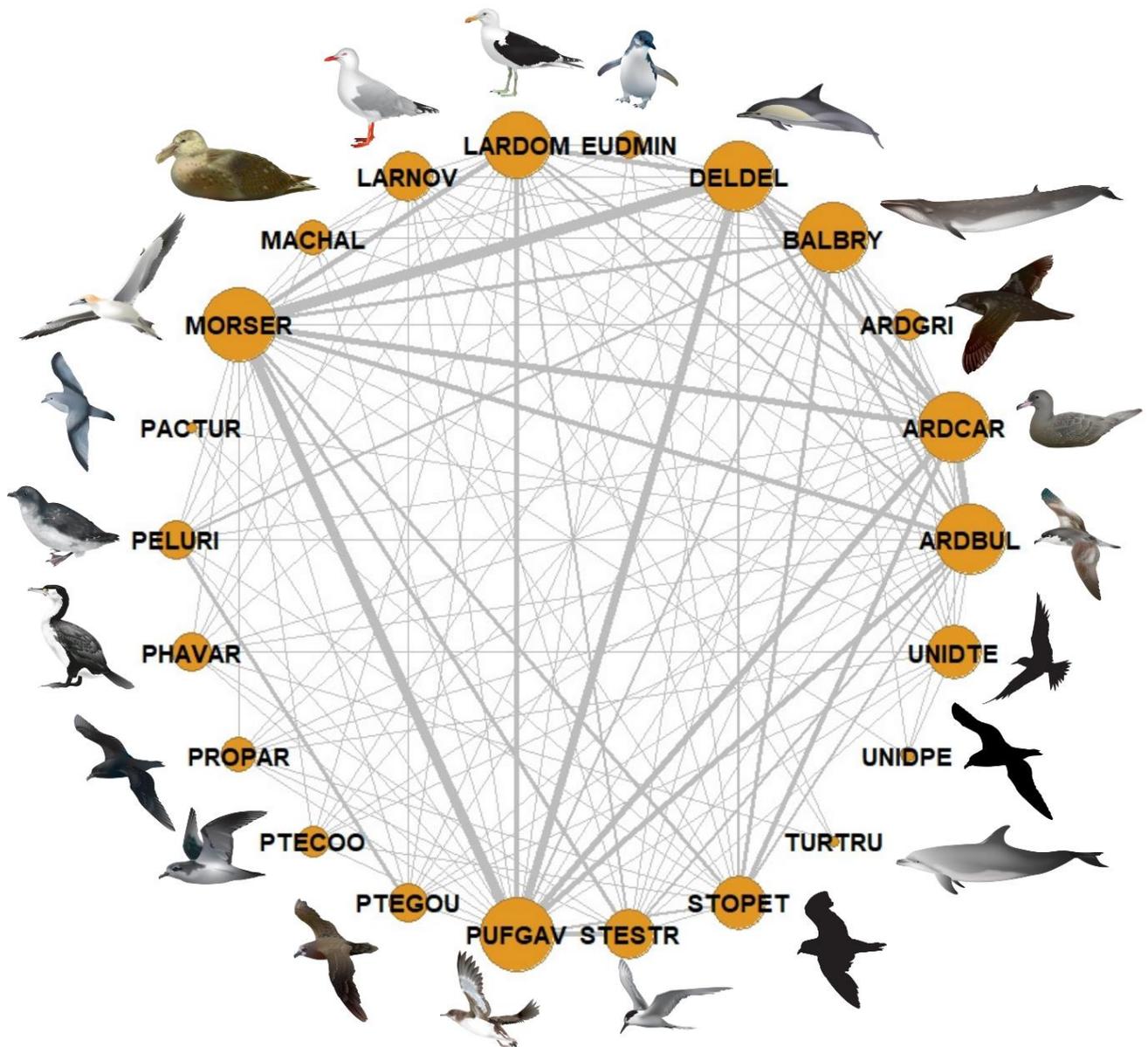


Figure 2.6 The social network of species associations within MSFA events ($n = 179$ MSFAs). Circle (node) width indicates weighted degrees (number of associates; Table 2.3), while line width is proportional to the association index between two species, with a wider line indicating a stronger association (Appendix 1).

Association indexes varied between species (Appendix 1) with the highest association indexes occurring between Australasian gannets and common dolphins (Index: 0.9), Australasian gannets and fluttering shearwaters (Index: 0.82), and fluttering shearwaters and common dolphins (Index: 0.7). These high association rates reflect their frequent attendance within MSFAs (Table 2.1). High association indexes were observed between Buller’s and flesh-footed shearwaters (Index: 0.61), flesh-footed shearwaters and common dolphins and Australasian gannets (Index: 0.59 for both species).

2.4 Discussion

Here we reveal the complex dynamics of associations within MSFA events in the Gulf. The complexities of communities that gather to forage on ephemeral prey patches are reflected in the eight clusters and species attendance and association patterns. There are clear patterns of foraging associations in the Gulf; specifically, we found that MSFA composition varied by season, with species attendance varying based on prey and movement patterns. Likewise, species-specific association patterns reflect diet and niche partitioning. By incorporating fine-scale attendance patterns and species-level seabird identification, we expanded on the findings of Gostischa *et al.* (2021) increasing from three MSFA clusters to eight, reflecting key associations within the Gulf. These updated clusters reflect current association patterns in the Gulf and foraging conditions. For example, the addition of Cluster a – Bryde’s whales and storm petrels – highlights the shift by Bryde’s whales from primarily fish prey to zooplankton (Carroll *et al.*, 2019; Gostischa *et al.*, 2021), most likely with changing prey availability in the Gulf (Pinkerton *et al.*, 2012).

Clusters included species that varied across various trophic levels, with those that characterise the cluster reflecting the key prey species present (Table 2.2). Some MSFAs were mixed trophic levels, with both planktivores and piscivores foraging together, suggesting the availability of multiple prey or scavenging on prey scraps (Au & Pitman, 1986; Olmos *et al.*, 2013). Using foraging ecologies and prey targeting, we generalised the clusters as planktivore, piscivore, multitrophic and scavenger based, with multitrophic being the most frequently encountered. These clusters involved both cetacean-seabird and seabird-only MSFA events, but we never encountered MSFAs with only cetaceans in attendance.

2.4.1 Factors influencing composition

Season

Group size increased with richness (number of species), suggesting a greater number of species may facilitate foraging opportunities for a greater number of individuals. MSFA taxonomic richness reflects hierarchical interactions and local enhancement, with greater prey accessibility and cue emittance likely attracting a greater number of individuals to an MSFA event (D’Amours *et al.*, 2008; Pöysä, 1992; Rouviere & Ruxton, 2022; Thiebault *et al.*, 2014). Seasonal shifts in group size further reflects associated shifts in prey availability and abundance which driving density-dependent group dynamics (Kent *et al.*, 2020; Stephenson *et al.*, in review; Uluduz *et al.*, 2020). Cooperative foraging and predator vigilance in social animals may increase their tendency to forage in large groups. However, predation-avoidance and prey associated benefits are likely species-specific and dependent on the species they associate with and oceanographic conditions (Gygax, 2002; Syme *et al.*, 2021). Group size further reflects MSFA conditions, with larger aggregations tending to persist longer due to prey patch maintenance and prey abundance (Cresswell & Quinn, 2011; Thiebault *et*

al., 2016; Veit *et al.*, 1993). Association patterns and clusters reflect species' foraging ecologies and prey specificity, with MSFA composition reflecting oceanographically driven shifts in prey availability and abundance, which in turn affects the distribution of marine predators in the Gulf (Carroll *et al.*, 2019; Chang *et al.*, 2003; Hamilton, 2020). Seasonal shifts in ocean temperatures, upwelling, and currents influence primary productivity and impact higher trophic levels through bottom-up effects (Benoit-Bird & McManus, 2012; Carroll *et al.*, 2019; Cox *et al.*, 2018; Thompson *et al.*, 2012). Prey flexibility allows predators to change prey species with changing foraging conditions, enabling them to engage in MSFA events across various seasons through the Gulf's waters (Stephenson *et al.*, in review).

Many seabirds and cetaceans occurring year-round are highly mobile generalist feeders, as a cohort foraging across various trophic levels in relation to prey availability, aggregating where prey is abundant (Dehnhard *et al.*, 2020; Hussey *et al.*, 2015; McClellan *et al.*, 2014). The most frequently observed species were social foragers (e.g., common dolphins and Australasian gannets), which show coordinated foraging, flocking, and/or movement behaviours (Giraldeau & Caraco, 2018; Jones *et al.*, 2018). The high proportion of common dolphins year-round across MSFAs aligns with previous Gulf studies (e.g., Stockin *et al.* 2008; Hamilton, 2020), which found that aggregations of common dolphins are found year-round in the Gulf. The Gulf's productive waters supported large dolphin foraging groups, with some aggregations involving over 500 dolphins foraging in association with seabirds, Bryde's whales and schooling fish. Bryde's whales were also found year-round, with their prey flexibility reflected in their attendance in both planktivore and piscivore MSFAs. Their movement throughout the Gulf reflects foraging plasticity and movement in response to changing prey availability and cues emitted from other foragers (Colbert, 2019; Hamilton, 2020; Izadi *et al.*, 2022). Bryde's whales were observed foraging alongside gannets and common dolphins, capitalising on dolphins' work, at times scattering or halting the MSFAs, which is consistent with previous studies (Baker & Madon, 2007; Izadi *et al.*, 2022). Our work furthers the findings of Gostischa *et al.*, (2021) through the identification of the Bryde's whale – storm petrel association (Cluster a) which reflects their dietary shift towards planktivorous prey with changing ocean conditions in the Gulf (Carroll *et al.* 2019; Pinkerton *et al.*, 2012). Despite this prey shift, Bryde's whales had a high association rate with many other species, often foraging in both piscivore and planktivore based MSFAs.

Movements and migrations

These MSFAs involved highly threatened and locally significant species, with the attendance of species and occurrence of clusters reflecting seasonal movements of both predators and prey (Gaskin & Rayner, 2013; Whitehead *et al.*, 2019). Species that remain in the Gulf year-round tend to be frequent attendees, with attendance varying with prey availability. Large rafts and feeding aggregations of fluttering shearwaters and white-fronted terns were found year-round in the inner gulf waters, frequently engaging in both fish and plankton MSFAs (Berg *et al.*, 2018; Gaskin, 2017; Gaskin & Rayner, 2013; Whitehead *et al.*, 2019). Gannets, like many seabirds, are top predators in marine

ecosystems, foraging across large distances in the Gulf. Gannets were found to forage in association with subsurface predators, including schooling fish and common dolphins year-round, with the Gulf providing their life needs throughout breeding and non-breeding seasons. Despite their wide-ranging foraging, gannets show foraging separation by colonies, with colony members utilising different areas of the Gulf's waters through local enhancement and information sharing (Adams, 2020; Machovsky-Capuska *et al.*, 2014). As data were collected throughout the Gulf's waters, we likely encountered gannets from different colonies throughout the study. While some gannets migrate during their first years of life, most stay within the Gulf's waters (Ismar *et al.*, 2011). We observed gannets in 120 MSFA events throughout the study period. Gannets were often foraging alongside common dolphins and/or schooling fish (Clusters h and d respectively) and were the most frequently encountered species during our surveys. Gannets are flexible foragers, with their diet of pelagic fish and squid reflecting changing prey availability and the ephemeral nature of prey patches in the Gulf (Adams, 2020).

The Gulf is an important habitat for many species, with many migrating to the Gulf's islands to breed. Species attendance within MSFA events reflects these migration patterns. For example, Buller's shearwaters were only observed during their September to May breeding season due to annual trans-equatorial migrations to the North Pacific Ocean (Marchant & Higgins, 1990). Buller's shearwaters breed solely on the Poor Knights Islands, foraging throughout the Gulf and other northern NZ waters (Gaskin & Rayner, 2013), aggregating at planktivore and piscivore MSFAs, surface feeding on small fishes and krill (Marchant & Higgins, 1990).

Low attendance at MSFAs is further explained through foraging ranges and movement, with long-distance foraging ranges outside the survey range. Migratory species include flesh-footed and sooty shearwaters and black petrels, which migrate to the north Pacific and eastern Pacific, respectively (Friesen *et al.*, 2017; Shaffer *et al.*, 2006). Sooty shearwaters' low attendance at MSFAs ($n = 7$) reflects their long foraging ranges, with breeding sooty shearwaters foraging offshore for multiple days, travelling distances 500 to 2000 km from colonies during long and short foraging bouts, respectively (Shaffer *et al.*, 2009). Sooty shearwaters are trans-equatorial migrants, accessing prey resources in both the Northern and Southern hemispheres; as such, they are absent from New Zealand's waters during their post and non-breeding seasons (Shaffer *et al.*, 2006). Migratory seabirds in low attendance also included the black petrels ($n = 4$), which are only present from the Gulf during their breeding period from October to May (Imber *et al.*, 2003; Marchant & Higgins, 1990).

Foraging ranges may also be attributed to low attendance patterns. For example, both black and Cook's petrels frequently forage in offshore, shelf-break, and pelagic habitats outside our study range (Gaskin, 2017; Rayner *et al.*, 2008). Despite the observed low attendance, black petrels forage in the outer Gulf in large numbers in association with false killer whales (*Pseudorca crassidens*), bottlenose

dolphins and long-finned pilot whales (*Globicephala melas*), highlighting the need for future studies to capture these more 'offshore' MSFA events (Zaeschmar *et al.*, 2013). These frequent associations with cetaceans reflect a scavenging relationship whereby the petrels will forage on prey scraps generated near the surface by foraging cetaceans (Camphuysen & Webb, 1999; Evans, 1982; Pitman & Ballance, 1992). Petrel-cetacean associations suggest that foraging with relatively large cetaceans may be more beneficial than foraging with common dolphins and piscivorous birds, which forage on relatively smaller prey and do not dismember their prey, creating fewer foraging opportunities for these seabirds (Certain *et al.*, 2011; Evans, 1982; Pitman & Ballance, 1992).

Low attendance by black and grey-faced petrels and sooty shearwaters may also be due to the timing of foraging activity, with these species taking advantage of prey resources at night, targeting bioluminescent prey during the night phase of vertical prey migrations (Gaskin & Rayner, 2013; Imber, 1973, 1976). Nocturnal foraging activity was not surveyed during this study; however, nocturnal foraging behaviours may indicate the presence of nocturnal MSFA clusters, which are linked to greater at-sea foraging opportunities (Dias *et al.*, 2012; Ravache *et al.*, 2020).

2.4.2 Frequent attendees and MSFA clusters

Seabird-cetacean associations

The most frequently observed cluster was piscivorous Cluster h which was characterised by the presence of Australasian gannets, common dolphins, and fluttering shearwaters. These species share the strongest social affinity index, highlighting their frequent co-occurrence and cooperative foraging behaviours, as shown in previous Gulf research (Gaskin & Rayner, 2013; Gostischa *et al.*, 2021; Purvin, 2015). Dolphin-seabird associations were not uncommon (67% of MSFA events), with association patterns reflecting foraging facilitation through prey herding behaviours (Benoit-Bird & Au, 2009; Scott *et al.*, 2012; Vaughn *et al.*, 2010). Seabirds may also act as long-range detection cues for other marine predators, transferring information through their high-flying and plunge-diving behaviours. The high contribution of gannets in Clusters d and h indicates that they may provide visual cues indicating prey presence, leading to local enhancement and aggregation of predators across various trophic levels (Machovsky-Capuska *et al.*, 2011b; Veit & Harrison, 2017).

Dolphin-seabird foraging associations are common in a range of species elsewhere in the world, reflecting the importance of sub-surface herders in facilitating foraging for surface foragers and depth-limited divers (Au & Pitman, 1986; Degradi *et al.*, 2014; Evans, 1982; Vaughn *et al.*, 2008). The active herding behaviours of dolphins counteract the vertical scattering effect of aerial predators, keeping the prey patch condensed and easily accessible (Benoit-Bird & Au, 2009; Vaughn *et al.*, 2011). When common dolphins are present, we expected that the MSFA is fish-based, with dolphins herding schools of fish to the surface, increasing prey accessibility for surface foraging seabirds (Au & Pitman, 1986; Camphuysen & Webb, 1999; Clua & Grosvalet, 2001). Prey herding and condensing by

common dolphins was evident through drone footage collected during these MSFA events (Unpublished drone footage, see Chapter 4). Associations between white-fronted terns and dolphins are also evident in both Hector's (*Cephalorhynchus hectori*) and dusky (*Lagenorhynchus obscurus*) dolphins (Bräger, 1998; Vaughn *et al.*, 2008). Hector's dolphins, dusky dolphins, and terns forage on small schooling fish (<10cm) in nearshore environments, such as anchovies (*Engraulis australis*), pilchards (*Sardinia neopilchardus*), and sprats (*Sprattus spp.*), with dolphin groups herding prey to the surface, within reach of the shallow, surface plucking terns (Miller *et al.*, 2013; Vaughn *et al.*, 2007). When both planktivores and piscivore predators were present, the prey available was likely multitrophic. Coordinated foraging between subsurface predators herding prey at various trophic levels increases prey accessibility for various trophic levels of predators; thus, diverse assemblages of species may be reliant on a range of drivers to facilitate foraging.

Seabird-fish associations

Schooling fish also play a role in keeping prey condensed, herding plankton prey to the surface. Cluster c does not involve dolphins and instead is representative of seabirds associating with shoaling fish schools (Gaskin, 2017). Seabird-fish associations are well-established, with fishermen using seabirds as indicators of fish presence (Montevecchi, 2001). In planktivore clusters, seabirds, including Buller's shearwaters and fairy prions (Cluster c), white-fronted terns, and fluttering shearwaters (Clusters d, e, f, and g) frequently foraged in association with schooling fish. These fish included trevally (*Pseudocaranx dentex*) and kahawai (*Arripis trutta*), which were observed driving small-bodied prey to the surface (Gaskin, 2017; Gaskin & Rayner, 2013; Unpublished drone footage, see Chapter 4 for drone methodology). Prey availability through associating with predatory fish was likely a driver behind the strong foraging associations between fluttering shearwaters and white-fronted terns; however, due to the nature of this study, we were not able to include schooling fish in cluster analysis.

Our study further built on Gostischa *et al.*'s (2021) findings by identifying a scavenger cluster (Cluster b), which involved black-backed and red-billed gulls. As scavengers, these species likely do not play a role in the generation and maintenance of MSFA events, instead following predators, feeding on prey discards, and exploiting herding behaviours (Degradi *et al.*, 2014). Despite this, red-billed gulls rely on MSFA events, foraging alongside shoaling fish to obtain high-quality food through surface plucking on herded prey alongside other Procellariiform species (Frost & Taylor, 2018; Gaskin, 2017). Both black-backed and red-billed gulls were frequently found in MSFAs in nearshore areas, often foraging on plankton patches and scavenging on discards, reflecting their generalist diet (Degradi *et al.*, 2014; Vaughn *et al.*, 2008).

2.4.3 Infrequent and non-attendees

In this study, we covered extensive areas of the Gulf and a wide range of MSFA events; however, we were not able to cover many of the inner coastal embayments and outer gulf pelagic areas – as

such, we may not have captured a representative sample of nearshore coastal and offshore pelagic MSFA events.

Nearshore, coastal MSFAs

Nearshore, coastal MSFAs would likely involve species that were not frequently (<5% MSFAs attended) encountered in observed MSFA events, such as penguins (n =7), shags (n = 7) and bottlenose dolphins (n = 2). Little blue penguins often joined MSFAs as small groups (1-3 individuals), foraging alongside conspecifics on the outskirts of MSFAs (Carroll *et al.*, 2017; Daniel *et al.*, 2007; Sutton *et al.*, 2015). Previous studies have found these penguins forage alongside multi-heterospecific predators, including subsurface sharks, whales and tuna, and other seabird species (McInnes & Pistorius, 2019; Sutton *et al.*, 2020). However, their diet is dominated by nearshore, pelagic schooling fishes and crustaceans, with prey size and type limited by their small size and local abundance of prey species (Fraser & Lalas, 2004). As they are primarily inshore foragers, their foraging ranges likely excluded them from the offshore MSFAs we predominantly surveyed (Poupart *et al.*, 2017). Cormorants were observed in low numbers in nearshore MSFAs. Cormorants were not found to initiate or maintain MSFAs; they used their highly flexible diving abilities to catch prey herded by subsurface predators and scavenge on discards (Cosolo *et al.*, 2010; Degradi *et al.*, 2014; Gostischa, 2020).

Infrequent attendees also included bottlenose dolphins (n = 2) which are nearshore, coastal foragers. Bottlenose and common dolphins were not observed foraging within the same MSFAs; this may be due to competitive exclusion, spatial foraging, niche partitioning and aggression between species (Dwyer *et al.*, 2016; Hamilton, 2020; Methion & Díaz López, 2021). Low attendance by bottlenose dolphins may be attributed to their nearshore foraging range, typically foraging in shallow coastal areas outside of the main search area of our surveys (Colbert, 2019; Dwyer *et al.*, 2014, 2016; Hamilton, 2020; Stephenson *et al.*, in review). However, despite this low attendance, bottlenose dolphins have been recorded foraging with other cetaceans, including false killer whales (*Pseudorca crassidens*, Zaeschmar *et al.*, 2013), common, striped (*Stenella coeruleoalba*), and spotted (*Stenella frontalis*) dolphins (Elliser & Herzing, 2016; Quérouil *et al.*, 2008). Subtle dolphin-dolphin associations thus may not have been detected due to their coastal foraging range being outside our survey area.

While sharks, pinnipeds and killer whales were observed during the surveys, none were involved in feeding aggregations; however, previous studies have found these predators involved in MSFAs (Gostischa, 2020; Hamilton, 2020). Exclusion due to aggression and predation risk towards other marine mammals, competitive exclusion and avoidance may be a driver of the lack of attendance in MSFAs by killer whales (Jefferson *et al.*, 1991; Visser, 1999). In New Zealand, killer whales target larger prey items, including sharks and marine mammals, suggesting they herd prey as a pod rather than initiating or joining MSFAs (Constantine *et al.*, 1998; Visser, 2005). This competitive-exclusion and predation risk likely drives avoidance by other cetaceans, hindering MSFA formation (Visser,

2000; Visser *et al.*, 2010). Both bottlenose dolphins and killer whales typically forage on nearshore prey. Their varied diets and foraging ranges suggest they are foraging more inshore, in MSFAs potentially not covered in our survey ranges (Colbert 2019; Hupman *et al.*, 2015; Stephenson *et al.*, 2020).

Offshore MSFAs

Our survey range also did not cover the outer Gulf waters; as such, we may have missed offshore and pelagic MSFA events. Spatial distribution of marine predators by Hamilton (2020) suggest that the outer Gulf and pelagic waters are a productive hotspot for marine predators across all seasons. The deeper, pelagic waters of the outer Gulf are associated with species not frequently observed in the observed MSFA events. While not observed during this study, bottlenose dolphins and false killer whales frequently forage in association with each other in the outer Gulf (Zaeschar *et al.*, 2013). Likewise, sharks and manta rays were not observed foraging in MSFA events. As the Gulf is an important habitat for sharks, we expect they may be engaging in MSFAs under the surface, out of view from the boat-based observations (Hamilton, 2020). Sharks and rays are highly mobile, making extensive use of the entire water column and moving in response to prey availability and oceanographic conditions (Barnett *et al.*, 2010; Francis *et al.*, 2019; Francis & Jones, 2016; Nicholson-Jack *et al.*, 2021). Giant petrels were occasionally observed ($n = 4$) foraging alongside other scavenging seabirds for prey, foraging on prey scraps from messy piscivorous foragers, aligning previous dietary studies (Copello *et al.*, 2008; González-Solís *et al.*, 2000, 2002). These petrels tend to occur in offshore areas at the continental shelf edge, with incursions inshore reflecting foraging and movement due to unfavourable weather (Gaskin & Rayner, 2013).

2.4.4 Conclusion

This chapter provides valuable insights into the fine-scale association patterns between seabirds and cetaceans in MSFAs the Gulf, revealing eight unique MSFA clusters. Clusters and association indices reflect prey availability, with species dietary specialisations providing insight into the prey type present. Clusters vary in frequency throughout the study, reflecting changing prey availability and oceanic conditions that influence prey movements and predators (Hamilton, 2020; Stephenson *et al.*, in review). One of the challenges of this study was capturing a representative sample of all MSFA types in the Gulf. While our study focused on seabirds and cetaceans, future studies would benefit from including inshore and offshore MSFA events that may capture associations with pinnipeds, mobulid rays, sharks, and large predatory fish. The species associations and MSFA clusters identified align with other findings on the importance of sub-surface predators on the foraging ecology of seabirds (Au & Pitman, 1986; Clua & Grosvalet, 2001; Vaughn *et al.*, 2008). The seabird-cetacean and seabird-seabird associations reflect mutualistic and commensal relationships, with feeding associations forming when utilising the same prey patches. Future research should consider ways to incorporate the fine-scale association patterns of seabirds, cetaceans, and predatory fish to fill the knowledge gaps identified in this study.

Chapter 3 Group behaviours within MSFA events

3.1 Introduction

A social group's activity budget is the result of both individual and group decisions, with time allocation decisions reflecting cost-benefit trade-offs that influence fitness through resource acquisition and allocation, and reproductive success (Dunbar *et al.*, 2009; Marshall *et al.*, 2012). Activity budgets can infer foraging conditions and mechanisms underpinning foraging behaviours. Both intrinsic and extrinsic factors influence activity budgets and energy partitioning, with resource supply and distribution influencing behavioural patterns. Behavioural activity budgets and responses of large marine animals can be interpreted as a continuum or as categorical states, with both discrete and obvious behaviours reflecting interactions between resource availability (Chivers *et al.*, 2012; Dunphy *et al.*, 2020), competition (Breed *et al.*, 2013), predation risk (Mougeot & Bretagnolle, 2000), human interactions and disturbances (Lusseau & Bejder, 2007; Pirota *et al.*, 2018), and reproductive states (Dunphy *et al.*, 2020; Karniski *et al.*, 2015; Rizzuto *et al.*, 2018). These highly coupled behavioural adaptations can also be used to assess the energetic costs and benefits associated with foraging and the mechanisms that enable marine predators to balance energy expenditure under changing environmental conditions (Cairns, 1988; Dunn *et al.*, 2020).

The investigation of activity budgets is a fundamental tool for understanding behavioural strategies and the predicted trade-offs between energy acquisition and expenditure across various environmental conditions and social environments (Grémillet *et al.*, 2012; Markones *et al.*, 2010). Activity budgets can indicate prey availability and energetic demands of various foraging strategies, providing a unique insight into ecosystem health and functionality (Cairns, 1988). While active foraging can be used as a proxy of prey availability and distribution, resting behaviours can indicate recovery from high energy costs incurred during foraging, and digestion of prey (Joyce *et al.*, 2017; Ropert-Coudert *et al.*, 2004), incubation of young and guarding of chicks (Osborne *et al.*, 2020), lactation and calf care (Bejder *et al.*, 2019) and passive movement in-between or after foraging events (Sánchez-Román *et al.*, 2019).

Intrinsic factors, including personality (Patrick & Weimerskirch, 2014), energy budgets (Lendvai *et al.*, 2004) and previous experience (Daunt *et al.*, 2007), influence the foraging strategy used by an individual. More efficient foragers have greater energy gained than expended, allowing for increased offspring provisioning and reproductive success (Daunt *et al.*, 2007; Jeanniard-du-Dot *et al.*, 2017). However, travel costs and competitive ability determine an individual's foraging efficiency and ability to travel to and forage within profitable prey patches and MSFAs (Ballance *et al.*, 1997). Many small predators are energetically constrained by the low caloric content of their food, with smaller

carnivores experiencing foraging constraints associated with vulnerability to predation and caloric balances (Rizzuto *et al.*, 2018). Among alcid, for example, smaller birds need to take in more calories in proportion to body weight than larger birds, with generalist diets and flexible foraging ecologies offsetting foraging and metabolic maintenance costs (Vermeer & Devito, 1986). Other predators, like dolphins (Benoit-Bird, 2004; Simonis *et al.*, 2017) and whales (Joyce *et al.*, 2017), may be time and depth limited, adjusting their foraging behaviours to follow the diel migration of their prey.

Different life history stages pose different energetic demands. Individuals with dependent offspring must ingest sufficient food to feed themselves and their offspring, whilst maintaining body condition. Central place foragers regularly commute between terrestrial breeding habitats and foraging grounds, balancing self and offspring provisioning and care (Burke & Montevecchi, 2009; Weimerskirch, 1998). Inter- and intra-specific competition by central-place foragers can result in depleted prey within the near-colony foraging area, a phenomenon known as 'Ashmole's halo', driving species to forage further from colonies in search of better foraging conditions (Ashmole, 1963; Weber *et al.*, 2021). For both seabirds and cetaceans, foraging ranges, surface intervals, habitat and trip duration vary with body condition, reproductive status, and predation risk, reflecting provisioning constraints associated with offspring care (Baumgartner & Mate, 2003; Srinivasan *et al.*, 2018; Weimerskirch, 1998; Weir *et al.*, 2008).

An animal's social environment affects its ability to find and capture food resources, with the presence and behaviour of con- and hetero-specifics influencing foraging behaviours and collective decision making (Farine *et al.*, 2014, 2015; Ward & Webster, 2016). Likewise, personal, and social information can shape the behaviour displayed, reflecting adaptive decision making and selective pressures for association patterns (Hämäläinen *et al.*, 2021; Jones *et al.*, 2018; Machovsky-Capuska *et al.*, 2014). Therefore, understanding these social dynamics is important for understanding the success of individuals, populations, and communities of animals. Using biodiversity metrics, such as richness and diversity, we can gain insight into the fine-scale interactions between species that influence the cost-benefit trade-offs of foraging within MSFA events (Costello *et al.*, 2004; Levine & HilleRisLambers, 2009). Richness reflects the number of species present within MSFA events, with species migration and movement patterns influencing the types of species present in given areas. Richness may be limited by niche overlap and competition between MSFA attendees (Alroy, 2018; Shurin & Allen, 2001). Diversity then takes these biodiversity analyses one step further to account for the number of each species, allowing us to review the potential drivers that support MSFA events, such as prey availability and abundance.

There are many different abiotic (e.g., upwelling; Raymond *et al.*, 2010 and Thompson *et al.*, 2012, currents; Byrnes *et al.*, 2021, and wind; De Pascalis *et al.*, 2020 and Pistorius *et al.*, 2015) and biotic

(e.g., prey movements; Gleiss *et al.*, 2013; Regular *et al.*, 2010) factors that influence resource distribution, abundance, and availability for marine predators. Foraging conditions have cascading effects on overall group behaviours, driving changes and trade-offs in activity budgets (Fattorini *et al.*, 2018; Martínez *et al.*, 2018). For example, social information on the location of ephemeral prey patches is essential for reducing time spent searching for prey and expending energy on searching behaviours (Thiebault *et al.*, 2014). However, foraging within MSFAs doesn't come without costs, and foraging alongside other marine predators can increase handling and chase time in some species and kleptoparasitism in others (Cansse *et al.*, 2020; García *et al.*, 2010). These costs can shape species interactions and involvement within MSFAs. MSFA composition and community dynamics are predicted to reflect the payoffs of social information and facilitative interactions (Goyert *et al.*, 2018a, 2018b; Hämäläinen *et al.*, 2021; Pajmans *et al.*, 2019). Social information and resource partitioning provide benefits in unpredictable and dynamic habitats, with information use driving the formation of social bonds, resource provisioning and enhanced prey detection at ephemeral prey patches (Hämäläinen *et al.*, 2021; Jones *et al.*, 2017; Robertson *et al.*, 2014). Joint decision making and synchronisation within groups can help maintain group cohesion and organisation to reduce unnecessary energy expenditure (Conradt & Roper, 2005). When prey predictability is lowered, activity budgets reflect the increased time and distance for prey to be detected, with buffered foraging duration, range and timing reflecting preferred prey availability (Litzow & Piatt, 2003) and species-specific foraging ecologies and flexibility (Cavallo *et al.*, 2020; Karkarey *et al.*, 2017; Ropert-Coudert *et al.*, 2004).

By understanding the intrinsic and extrinsic factors that drive these activity patterns, we can better understand why species forage within MSFAs, not only for ecological understanding but also for conservation management and planning (Burke & Montevecchi, 2009; Camphuysen *et al.*, 2012; Montevecchi, 2007). Foraging behaviours and time allocation can be used to predict and prevent human-wildlife conflicts and the interruption of foraging events (Sbragaglia *et al.*, 2021; van Beest *et al.*, 2019). High-trophic level species are valuable ecological indicators, with cumulative environmental and anthropogenic stressors being reflected through changes in foraging behaviour and energy budgets across various trophic level predators (Cairns, 1988; Furness & Camphuysen, 1997; Hazen *et al.*, 2019; Wallace *et al.*, 2018).

With changing ocean and foraging conditions, understanding species interactions and behavioural activity budgets will allow us better to understand the predator-prey and predator-predator dynamics, environmental constraints and changing food web dynamics influencing MSFAs (Gostischa *et al.*, 2021; Wallace *et al.*, 2018). Here, we use group activity budgets within MSFA events, with the addition of season and community dynamics (Clusters; Table 2.1), to investigate species-level patterns of foraging behaviours within MSFA events.

3.2 Methods

See Chapter Two (Sections 2.1 and 2.2) for study location and sampling methodology.

3.2.1 Behavioural observations

Boat-based, focal group field observations of seabird and cetacean foraging behaviours and associations were collected during MSFA events encountered during non-systematic surveys of the Gulf. Data were collected from the University of Auckland 15 m vessel *RV Hawere* and the Auckland Whale and Dolphin Safari (AWADS) 20m whale watch vessel *MV Dolphin Explorer*. As in Chapter two, MSFA events were defined as aggregations of two or more species foraging in the same prey patch. During these events, behavioural data for all species present in the MSFA were recorded once the research vessel was within ~400m of the focal group. Species identification and behavioural states were quantified using focal group observations with the help of binoculars and tablets for data recording. Upon arrival at an MSFA event, a focal group follow method was used to collect data on all species and their behaviours within the MSFA. The primary observer continuously scanned the whole MSFA to systematically record behavioural events, the estimated number of individuals for each species and the proportion of individuals in the different behavioural states as defined in Table 3.1.

During surveys, the following three variables were recorded: (1) Duration - time the group displayed recorded behaviours (generated using timestamps in data entry) during the MSFA. Durations were best estimates and contained elements of human error. (2) Proportion of group - percentage of the group engaged in different behaviours. (3) Number of individuals - count, or best estimate of the number of individuals in each species present. Behavioural data were collected continuously, with changes in the behavioural states of the different species recorded throughout the observation period. Data collection stopped when the MSFA dissipated or in those situations where the MSFA activity was repetitive and persistent over periods of more than ~45-60 minutes, and we were confident that a representative sample of the event was collected. Due to AWADS targeting marine mammals, the vessel did not stop for seabird only MSFA events. Thus, the activity budgets are representative of the behaviours displayed during the time the MSFA was visible from the vessel, with behaviours recorded to the best of our ability with the assistance of binoculars.

The ethogram (Table 3.1) describes 29 different behaviours observed within MSFA events. These descriptions are modified from previous behavioural studies on cetaceans and seabirds (i.e., Camphuysen & Garthe, 2004, Stockin *et al.*, 2009 and Würsig & Pearson, 2014). Behavioural states (Table 3.1) were categorised as (a) 'foraging' when individuals are actively searching for and obtaining prey, (b) 'non-active non-foraging', when individuals were engaging in non-active behaviours to conserve energy, and (c) 'active non-foraging', active behaviours which are not associated with foraging.

Table 3.1 Overview of behaviours of cetaceans and seabirds within multi-species foraging associations.

State	Taxa	Group Behaviour	Description
Foraging	Seabirds	High and low diving	Diving into the water from above the surface from various heights. Primarily used by piscivores.
		Surface plucking /dipping	Picking prey from the water's surface by hovering above or dipping head under the water. Primarily used by planktivores.
		Pursuit diving	Swimming under the water to chase prey.
	Cetacean	Bubble-net	Release of bubbles while swimming to potentially entrap and aggregate prey.
		Lunging	Specific for baleen whales. Rushing motion in the water to engulf prey, mouth extended to engulf water-laden prey.
		Head/tail slaps	Breach and slap of head on the surface of the water. Tail flukes or head raised above the surface and ventral or lateral side slapped down.
		Rushing/ Chasing	Rushing motion in the water to capture or engulf prey.
Non-active non-foraging	Seabird	Rafting	Sitting in a large single species group.
		Sitting	Sitting on the surface of the water.
	Cetacean	Milling	Directionless movement patterns, no net movement in any specific direction by individuals or the group.
		Resting	Logging or slow, regular surfacing. Little evidence of forward movement, surfacing is more predictable and exhalations are quiet
Active non-foraging	Seabird	Travelling	Flying in a single direction.
		Approaching	Flying towards the MSFA.
		Circling	Circling seabirds, frequently with head down while flying
		Zig zagging	Flying as a coordinated group, often following subsurface prey
		Chasing	Flying at/towards other seabirds, not associated with chasing prey
	Cetaceans	Surfacing	Surfacing to breathe
		Diving	Following breath on the surface, back is arched high, and animal disappears from view for a prolonged period (>1min).
		Travelling	Engaging in persistent, directional movement, spacing is varied, and individuals swim with short, constant sub-surface intervals.
		Socialising	Interactive events, tactile contact between individuals. Chasing, leaping, and/or engaging in physical contact.
		Bow riding	Positioning themselves in the bow pressure wave of a moving vessel.
		Fast travel	The entire body leaves the water, continuous jumping over >2 body lengths, fast travel
		Mating	Belly to belly contact
		Nursing	Calf positions itself under the mother and turns to suckle at the mammary slits.

3.2.2 Activity budget calculation

Using the group focal follow data, MSFA activity budgets were generated for each species. Using time stamps, sample intervals were used as indicators of the ‘duration’ of time the group spent in different behavioural states, throughout the MSFA. To minimise the effects of group size, the proportion of the group (number of individuals performing behaviours in respect to the sum of individuals; from 0- none performed behaviour to 1- all performed behaviour) was used. These proportions were then used to summarise the group's engagement in each of the three behavioural states: foraging, active non-foraging, and non-active non-foraging. Using the proportions for each sample interval, an overall sum of the proportion of time spent in each of the behavioural states throughout the MSFA duration was generated for each species group.

3.2.3 Data analysis

The proportion of time species spent in each behavioural state was analysed with a series of generalised linear models (GLM) of the quasi-binomial error distribution for 0-1 proportion data, weighted by the mean group size of each species within MSFA events. GLM's tested both continuous and categorical fixed effects (See Table 3.2).

Table 3.2 Fixed effects tested using GLM's

Factor	Levels	Categories
Season	4	Summer: December - January Autumn: March-May Winter: June – August Spring: September – November
Species	22	See chapter 2, Table 2.1
Cluster	8	a, b, c, d, e, f, g and h (See chapter 2, Table 2.2)
Duration	Numerical	The total duration of the MSFA event (minutes)
Diversity	Numerical	Shannon-Weiner Diversity Index. See Chapter Two, Equation 1.2.
Richness	Numerical	Margalef Richness Index. See Chapter Two, Equation 1.1.

All analyses and visualisation were conducted in R-studio (version 1.4.1717) using the packages tidyverse (Wickham *et al.*, 2019), ‘emmeans’ (Lenth, 2021) and ‘plyr’ (Wickham, 2011). The significance level, using $p \leq 0.05$ of each explanatory categorical variable, was investigated using analysis of variance (Chi-squared ANOVA) and pairwise comparisons (Lenth, 2021). Overall activity budget GLMs were carried out with the inclusion of all species. However, when comparing factors at a species level, only species observed in more than 5% of MSFAs were included (See Table 2.1;

hereafter, 'frequently occurring species'). The analysis of only foraging, active non-foraging and non-active non-foraging allowed us to understand meaningful metrics of MSFA activities whilst acknowledging that species are not always engaging in the MSFA event. The analysis of only frequently attending species facilitated data analysis and visualisation, as sample sizes of some individual species were too small to generate meaningful data. Linear models were also used to examine the relationship between species group size (See Table 2.1 for species and group size) and the proportion of time species spent in each behavioural state. Group size (mean number of individuals of each species) was instead used as a weight in all GLM's in this chapter. GLM's testing the significance of the following variables: species, diversity, duration, richness and season were applied to data filtered by cluster and species to allow for within-cluster and within-species differences to be investigated.

3.3 Results

A total of 179 MSFA events were analysed, with a cumulative total of 55.4 hours of behavioural observations. The duration of behavioural data collected per MSFA event ranged from 1-109 minutes (mean \pm SE = 18.07 \pm 1.36 min). Our dataset represents 28,346 individuals from 22 species across 179 MSFA events. When assessing the proportion of the MSFA event species groups spent in each behavioural state, active foraging varied by cluster, species, and season (GLM, ANOVA, $p < 0.05$). Active non-foraging varied (GLM, ANOVA, $p < 0.05$) by cluster, species, duration, and richness. Furthermore, non-active non-foraging varied (GLM, ANOVA, $p < 0.05$) with cluster, diversity, and richness. When assessing the influence of group size using linear models (LM; estimate \pm SE), the proportion of time a group spent active foraging (0.05 ± 0.01 , $p < 0.001$) and non-active non-foraging (0.02 ± 0.01 ; $p = 0.02$) were found to increase with group size. Active non-foraging, however, did not vary with group size ($p > 0.05$). All analyses from hereon only include frequently attending species (attendance in $>5\%$ MSFA events).

3.3.1 Individual species

Species-specific variation in behavioural activity budgets highlights the need for understanding underlying factors influencing observed behaviours. The proportion of time spent in the behavioural states varies by species (Table 3.3), with planktivores (e.g., white-fronted terns, fluttering shearwaters, and storm petrels) spending more time actively foraging than piscivores (i.e., common dolphins, flesh-footed shearwaters, and gannets).

Table 3.3 Summary statistics (average \pm SE) of proportion of MSFA event spent in each behavioural state for frequently attending species.

Species		Foraging	Active non-foraging	Non-active non-foraging
ARDBUL	Buller's shearwater	0.44 \pm 0.046	0.08 \pm 0.029	0.19 \pm 0.034
ARDCAR	Flesh-footed shearwater	0.13 \pm 0.028	0.46 \pm 0.041	0.20 \pm 0.031
BALBRY	Bryde's whale	0.17 \pm 0.035	0.43 \pm 0.060	0.26 \pm 0.056
DELDEL	Common dolphin	0.28 \pm 0.032	0.40 \pm 0.035	0.26 \pm 0.032
LARDOM	Black-backed gull	0.12 \pm 0.055	0.33 \pm 0.053	0.03 \pm 0.023
LARNOV	Red-billed gull	0.22 \pm 0.106	0.32 \pm 0.097	0.07 \pm 0.071
MORSER	Australasian gannet	0.21 \pm 0.024	0.44 \pm 0.028	0.28 \pm 0.027
PUFGAV	Fluttering shearwater	0.36 \pm 0.036	0.32 \pm 0.032	0.18 \pm 0.025
STESTR	White-fronted tern	0.55 \pm 0.063	0.24 \pm 0.049	0.03 \pm 0.017
STOPET	Storm petrel	0.40 \pm 0.078	0.06 \pm 0.026	0.08 \pm 0.048

GLM analysis of all data highlight that the proportion of the MSFA event groups spent foraging, active non-foraging and non-active non-foraging vary between species (GLM; ANOVA; $p < 0.05$). These differences in proportions of time spent in the three behavioural states are particularly evident when comparing box and whisker plots of the proportion of time spent in each behavioural state per MSFA event (Figure 3.1).

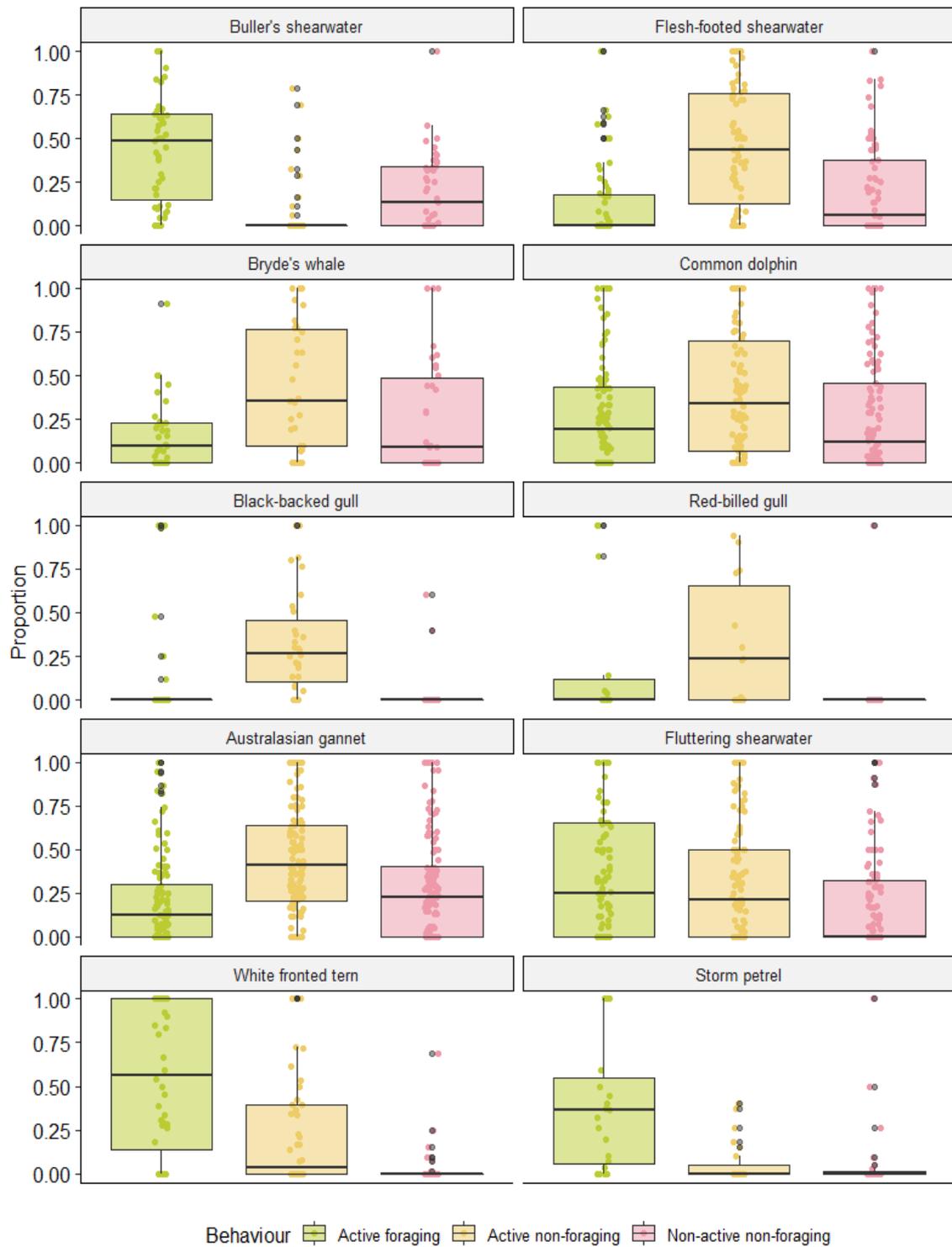


Figure 3.1 Box and whisker plot of the proportion of time frequently attending species (>5% MSFAs) spent foraging, active non-foraging, and non-active non-foraging within MSFA events (n = 179). The middle of the box indicates median (50% quantile), with lower and upper hinges showing 25% and 75% quantiles, respectively. Data beyond the whiskers are “outliers” and plotted individually as dark grey points.

Individual GLM's for the frequently attending species (>5% of MSFAs) further found that the proportion of time spent in the three behavioural states varied by diversity (Shannon-Weiner index; Equation 2.1), richness (Margalef's richness index; Equation 2.2) and total duration of the MSFA event.

Table 3.4 Summary of significant continuous GLM variables (diversity, duration, and richness; $p < 0.05$) for frequently attending species (>5% MSFAs) for the behavioural states. The effects of these significant factors increase (+) or decrease (-) the proportion of time groups spent in that behavioural state.

Species		Factor	Foraging	Active non-foraging	Non-active non-foraging
ARDBUL	Buller's shearwater	Diversity	-		
		Duration	+		
ARDCAR	Flesh-footed shearwater	Richness			+
BALBRY	Bryde's whale	Diversity	+		
DELDEL	Common dolphins	Diversity	+		-
		Duration	+		-
		Richness	-		+
LARDOM	Black-backed gull	Diversity		-	-
		Duration			+
		Richness			-
LARNOV	Red-billed gull	Diversity	+		+
		Duration	-		-
		Richness	+		-
MORSER	Australasian gannets	Diversity		-	
		Richness	+		
PUFGAV	Fluttering shearwater	Diversity		+	-

3.3.2 Season

Season was identified as a significant factor influencing the proportion of time groups spent foraging (GLM, ANOVA; $p = 0.004$), but not active non-foraging and non-active non-foraging (GLM, ANOVA; $p > 0.05$). When investigating the influence of season on the proportion of time groups spent foraging, autumn MSFA participants spent significantly less time foraging than spring ($p = 0.01$), summer ($p = 0.007$), and winter ($p = 0.05$), all other pairwise comparisons for foraging were non-significant ($p > 0.05$). No statistically significant pairwise differences ($p > 0.05$) were found when comparing the proportion of time groups spent in non-active non-foraging and active non-foraging behaviours.

When investigating within-season variation in behavioural states by frequently attending species, season influenced (GLM, ANOVA, $p < 0.05$) the proportion of the MSFA spent foraging for black-backed gulls (*Larus dominicus*, LARDOM), common dolphins (*Delphinus delphis*, DELDEL), flesh-footed shearwaters (*Ardenna carneipes*, ARDCAR), Australasian gannets (*Morus serrator*, MORSER) and red-billed gulls (*Larus novaehollandiae*, LARNOV). Non-foraging non-active behaviours varied with season ($p < 0.05$) for black-backed gulls, Buller's shearwaters (*Ardenna bulleri*, ARDBUL), flesh-footed shearwaters and storm petrels (Combination of *Pelagodroma marina* and *Fregetta maoriana*, STOPET), see Chapter Two, 2.2 Methodology). Active non-foraging behaviours varied with season ($p < 0.05$) for black-backed gulls, Buller's shearwaters, common dolphins and Australasian gannets. Season, however, was not a significant factor (GLM ANOVA, $p > 0.05$) affecting the proportion of time spent in the three behavioural states for Bryde's whales (*Balaenoptera edeni brydei*, BALBRY), fluttering shearwaters (*Puffinus gavia*, PUGGAV) and white-fronted terns (*Sterna striata*, STISTR).

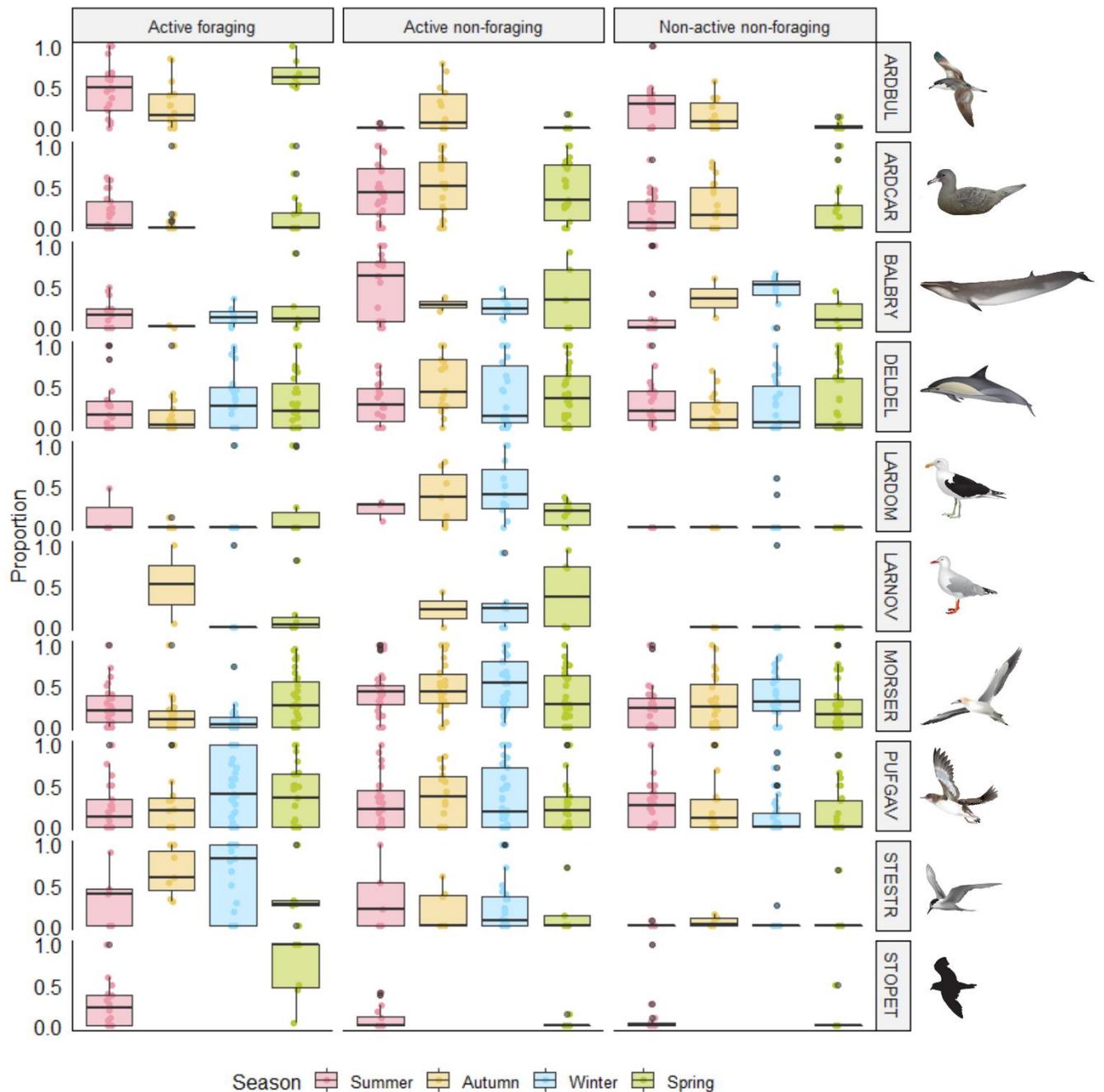


Figure 3.2 The proportion of time frequently attending species (>5% MSFAs; for species codes and attendance see Table 2.1) spent foraging, active non-foraging, and non-active non-foraging within MSFA events by season ($n = 4$). The middle of the box indicates median (50% quantile), with lower and upper hinges showing 25% and 75% quantiles, respectively. Data beyond the whiskers are “outliers” and plotted individually as dark grey points.

Pairwise comparisons revealed a significant difference ($p < 0.05$) between seasons for foraging, non-foraging non-active and active non-foraging for black-backed gulls, Buller’s shearwaters, common dolphins, Australasian gannets, and red-billed gulls. However, no significant differences ($p > 0.05$) between seasons were found for Bryde’s whales, fluttering shearwaters, flesh-footed shearwaters, storm petrels, and white-fronted terns.

Table 3.5 Summary of significant pairwise comparisons ($p < 0.05$) of seasons ($n = 4$) by frequently attending species ($>5\%$ MSFAs) for behavioural states. The first seasons listed have a greater (+) or lesser (-) proportion of time spent in that behavioural state than the second listed season.

Species		Season pairs	Foraging	Active non-foraging	Non-active non-foraging
ARDBUL	Buller's shearwater	Autumn – Summer			–
		Autumn - Winter		+	
DELDEL	Common dolphin	Spring - Winter		+	
		Autumn - Spring		+	+
LARDOM	Black-backed gull	Autumn - Summer			–
		Spring - Summer			–
		Spring - Winter			–
		Summer - Winter			+
		Autumn - Spring	–	+	
MORSER	Australasian gannet	Autumn - Summer	–		
		Spring - Winter	+	–	
		Summer - Winter	+		
		Autumn - Spring	+	+	
LARNOV	Red-billed gull	Autumn - Winter	+	+	
		Spring - Winter	–	+	

3.3.3 Cluster and species

As discussed in Chapter 2.4 (Discussion), clusters are valuable indicators of MSFA community structure. Here, we investigated the variation in the proportion of time groups spent in these behavioural states in each cluster (See Table 2.2 for cluster composition). GLM analysis of all data points highlighted that cluster is a significant factor (GLM; ANOVA; $p < 0.05$), influencing the proportion of time groups spent foraging, non-active non-foraging, and active non-foraging. From this overall GLM, pairwise comparisons revealed that Clusters a, d and h spent less time foraging than e, f, and g ($p < 0.05$), and Cluster c spent more time foraging than a, d, and h ($p < 0.01$). Cluster e spent less time 'active non-foraging' than Clusters d and h ($p < 0.001$). Likewise, those in Cluster e spent less time 'non-active non-foraging' than Cluster h ($p < 0.05$).

When investigating within-cluster seasonal differences, three (b, d and h) of the eight clusters showed significant differences. ANOVA analysis revealed that season was a significant factor by itself influencing foraging ($p < 0.001$) in Clusters b, d and h, non-active non-foraging ($p = 0.01$) in Cluster h and active non-foraging ($p = 0.0003$) in Clusters d and h. However, season was not a factor

influencing activity budgets for Clusters a, c, e, f, and g ($p > 0.05$). Pairwise comparisons found significant differences ($p < 0.05$) between season pairs in clusters b, d, g and h (Table 3.6).

Table 3.6 Summary of significant pairwise comparisons ($p < 0.05$) of seasons by cluster ($n = 8$) for behavioural states. First season listed has a greater (+) or lesser (-) proportion of time compared to the second season listed

Cluster	Season pairs	Foraging	Active non-foraging	Non-active non-foraging
b	Autumn - Spring	-		
	Autumn - Winter	-		
	Spring - Winter	-		
d	Autumn - Winter	+		
g	Spring - Summer	-	+	+
h	Autumn - Spring	-	+	
	Autumn - Summer	-	+	
	Autumn - Winter	-	+	

Using GLM's for each of the frequently attending (>5% MSFA events) species, we found that cluster influenced (GLM, ANOVA; $p < 0.05$) the proportion of time groups spent engaging in all three behavioural states for Buller's shearwaters, black-backed gulls, and fluttering shearwaters. Foraging and non-active non-foraging were found to vary by cluster for red-billed gulls. For common dolphins, however, only foraging varied by cluster ($p < 0.05$). Non-active non-foraging was found to vary by cluster ($p < 0.05$) for flesh-footed shearwaters, white-fronted terns, and storm petrels. And likewise, Bryde's whales showed significant cluster differences for active non-foraging ($p = 0.03$). No relationships between clusters and the proportion of time spent in each behavioural state (GLM, ANOVA; $p > 0.05$) were found for Australasian gannets. The proportion of time each species spends in the different behavioural states is highly variable between both species and clusters (Figure 3.3).

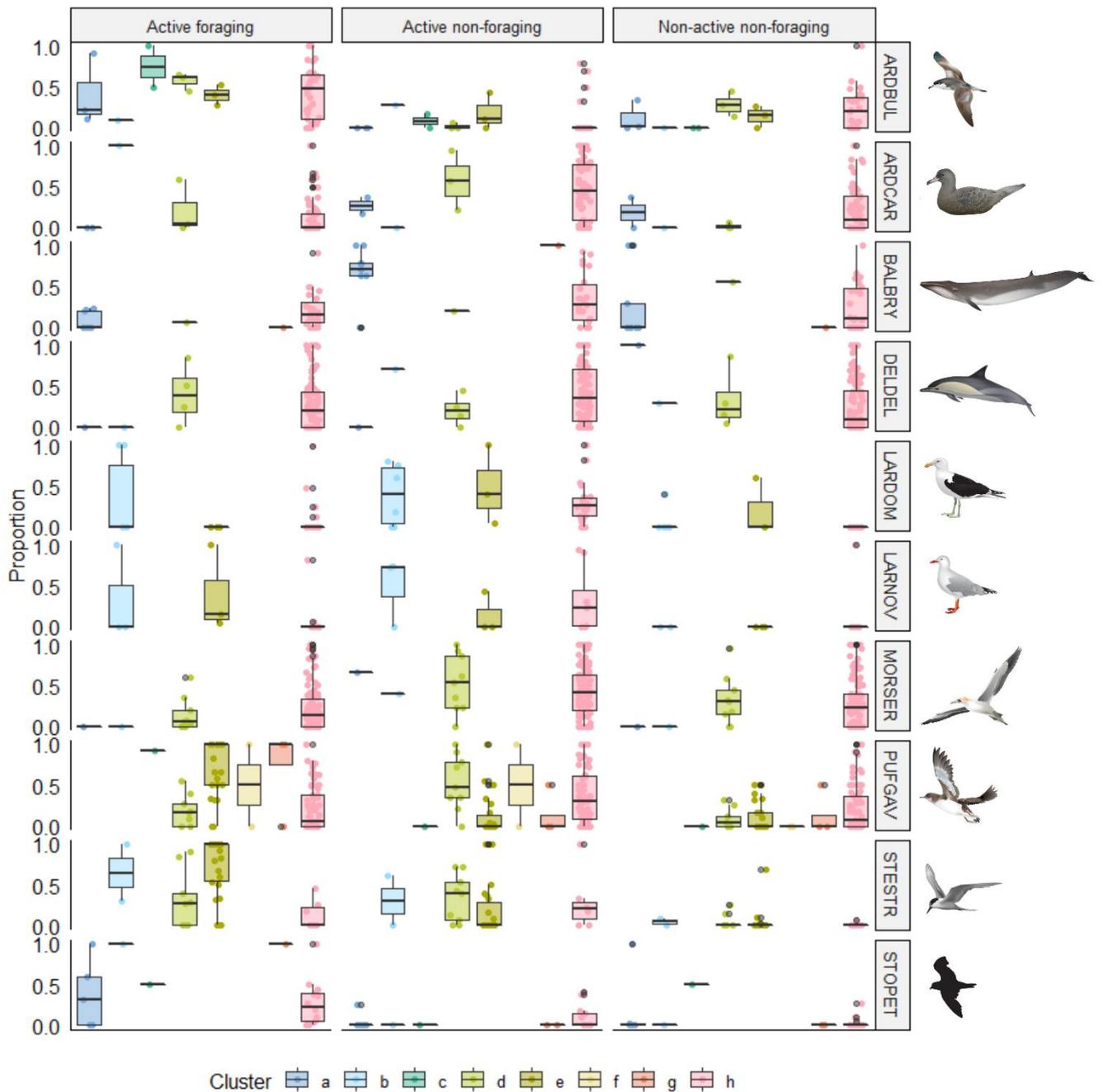


Figure 3.3 The proportion of time frequently attending species (>5% MSFAs; for species codes and attendance see Table 3.4) spent foraging, active non-foraging, non-active non-foraging and absent within MSFA events across the eight clusters (a - h). The middle of the box indicates median (50% quantile), with lower and upper hinges showing 25% and 75% quantiles, respectively. Data beyond the whiskers are “outliers” and plotted individually as dark grey points.

Pairwise comparisons of foraging behaviours for frequently attending species within clusters revealed that black-backed and red-billed gulls spent a greater proportion of time foraging in Clusters b and e than h ($p < 0.05$). Fluttering shearwaters spent more time foraging in Clusters e and g than d and h ($p < 0.01$) and more time active non-foraging behaviours in Clusters e than d and h ($p < 0.01$). All active non-foraging cluster pairs were non-significant ($p > 0.05$). No significant cluster pairs were

found for Bryde's whales, Buller's shearwaters, common dolphins, flesh-footed shearwaters, Australasian gannets, storm petrels and white-fronted terns ($p > 0.05$).

3.4 Discussion

Here we reveal the complexity of foraging behaviours within MSFA events depending on the season and types of communities formed by seabirds and cetaceans in the Gulf. In this study, MSFAs were already active when surveys began; thus, we recorded species' activity budgets during the maintenance, facilitation, and termination phases of the MSFAs (Clua & Grosvalet, 2001). Depending on the community of animals that gather (here reflected in the eight clusters) and the season the MSFA was sighted, the behaviours of MSFA participants vary widely. Yet, there are some clear patterns in the Gulf. Planktivores and piscivores, in particular, show significant differences during MSFA events, with planktivores spending more time actively foraging than piscivores, as is further reflected in the overall behaviours undertaken by cluster.

3.4.1 Influence of richness and diversity on behaviours:

Here, we used two different measures of biodiversity to assess MSFA activity budget dynamics, with richness and diversity reflecting the outcome of the behavioural interactions that drive the formation of MSFA events (Costello *et al.*, 2004). From this analysis, richness and diversity had variable effects on the behaviours within MSFAs. Diversity reflects migration patterns, with individual species filling MSFA roles open throughout different seasons. As species migrate to the Gulf for breeding (i.e., Buller's, sooty and flesh-footed shearwaters, fairy prion and black petrel), they fill various roles within MSFAs, with MSFA interactions affecting foraging conditions (Gaskin & Rayner, 2013). Under increasing richness (number of species), the proportion of time spent foraging increased for gannets and red-billed gulls but decreased for common dolphins. Richness may indicate prey being available at multiple trophic levels, with greater prey available for flexible foraging gannets and scavenging, plankton feeding red-billed gulls (Gaskin & Adams, 2018; Gaskin, 2021). Likewise, an increase in diversity may reflect a greater abundance and diversity of prey, with the aggregation of prey at different trophic levels supporting greater numbers of species. Increased resource availability and diversity support more diverse predator compositions until a predator-prey diversity equilibrium is reached and foraging behaviours are constrained (Shurin & Allen, 2001; Fox, 2007; Yang *et al.*, 2018). However, under increased richness, flesh-footed shearwaters spent more time non-active, non-foraging and active non-foraging. Flesh-footed shearwaters are relatively large seabirds and thus may face more energetic costs associated with take-off and flying, therefore spending more time doing non-foraging behaviours when richness, and hence potential prey competition, increased (Sakamoto *et al.*, 2013; Weimerskirch *et al.*, 2000).

While richness is an indicator of the number of species present, the diversity index reflects the number of each species in the community. The functionality of these MSFA events is dependent on

the niche and functional similarity between species and associated niche partitioning, or lack thereof. Higher quality prey patches strongly affect MSFA dynamics, with prey patch size, type, and abundance supporting a more diverse community of species (i.e., Vélková *et al.*, 2021). Prey diversity also shaped predator niche variation, with greater prey availability supporting a greater variety of species' trophic and foraging niches within MSFA events (Sánchez-Hernández *et al.*, 2021; Fox, 2007).

A greater allocation of time to foraging under increased diversity likely helps these animals counteract the effects of other predators feeding on the prey patch, potentially dispersing the prey patch. For example, diversity increased the proportion of time spent foraging in Bryde's whales, common dolphins, and red-billed gulls. Under increased diversity, common dolphins and Bryde's whales spent more time foraging, suggesting that greater prey patch quality and availability influences activity, resulting in increased time spent foraging in MSFAs. However, with greater species diversity may come increased competition for prey and disruption of common dolphin herding behaviours. With a greater variety of species targeting a prey patch, dolphins may need to work harder to maintain the prey patch and counteract the scattering effect of diving seabirds, lunge feeding Bryde's whales and sub-surface fish predators (Evans, 1982; Scott *et al.*, 2012; Vaughn *et al.*, 2008). Likewise, gannets showed increased foraging with richness, with increased diving frequency and height acting as a proxy for prey availability and depth. Thus species-rich MSFAs may indicate greater prey availability and foraging opportunities for gannets, with prey availability offsetting energetic costs attributed to plunge diving and take off (Bennison *et al.*, 2022; Machovsky-Capuska *et al.*, 2011b; Purvin, 2015).

Red-billed gulls did not have an important role in maintaining MSFA events. Gulls' heightened foraging under increased diversity likely reflects greater opportunities for kleptoparasitism (Brockmann & Barnard, 1979; Gaglio *et al.*, 2018b), facilitated plankton foraging by sub-surface prey herders and opportunistic foraging on increased food scraps from messy feeders (Kozmian-Ledward *et al.*, 2020). This generalisation may also hold for black-backed gulls. Black-backed gulls spent more time foraging in summer and spring, and red-billed gulls spent more time foraging in autumn; these differences are likely due to their different foraging strategies, with black-backed gulls primarily being surface feeders targeting pelagic fishes and red-billed gulls foraging on zooplankton (Baptist *et al.*, 2019; Mills *et al.*, 2008). For this reason, their foraging is likely dependent on both provisioning and local prey availability. While we could not quantify foraging success, the proportion of successful foraging attempts by gulls would also likely decrease with increasing MSFA richness, as shown with other scavengers (Maynard *et al.*, 2020). Scavenging birds, like gulls, black and giant petrels, are dependent on the foraging of associated species, with messy feeders providing carrion which does not require a significant amount of time to pursue and capture (González-Solís & Croxall, 2005; González-Solís *et al.*, 2000; Zaeschmar *et al.*, 2013).

3.4.2 Behavioural budgets of frequently attending species

As shown in Chapter two, species attendance within MSFAs is dependent on a range of factors, including their foraging ecology, migration patterns, and availability of preferred prey. Time constraints and species activity budgets are important focuses in behavioural research, with individuals balancing trade-offs between sociality, physiology, energetic needs and predation risk (Courbin *et al.*, 2022; Tremblay *et al.*, 2022; Wirsing *et al.*, 2008). In different conditions, individuals shift their behavioural budgets. When comparing overall trends in the Gulf, we demonstrate that planktivores spent more time actively foraging than piscivores, which comparatively spent more time in active non-foraging behaviours. An exception to this generalisation is Bryde's whales which forage on both zooplankton and fish prey, although they are increasingly targeting zooplankton, and plankton MSFA events, with shifts in the Gulf's health (Carroll *et al.*, 2019; Gostischa *et al.*, 2021; Izadi *et al.*, 2022). Bryde's whales were found to spend less time foraging than planktivorous seabirds due to their different foraging techniques and associated energetic costs. Bryde's whales use an energetically expensive lunge feeding strategy (Izadi *et al.*, 2022; Potvin *et al.*, 2021) and, thus, spent more time engaged in active non-foraging than foraging behaviours. While foraging rates were low across seasons, Bryde's whales spent more time in an active non-foraging behavioural state, such as travelling and diving, in spring and summer and a non-active non-foraging state, such as milling, in autumn and winter. These behavioural differences are likely due to shifts in preferred prey independent of seasonal prey availability (Carroll *et al.*, 2019). Within MSFAs, we saw Bryde's whales lunging multiple times within prey patches, leaving once the prey patch had been diminished or widely scattered, and foraging was no longer energetically affordable (Izadi *et al.*, 2022).

3.4.3 Influence of season on activity budgets

Extrinsic drivers of seasonal variation

Marine predator foraging dynamics are reliable indicators of cumulative ecosystem stressors and changes (Fayet *et al.*, 2017; Gulka *et al.*, 2020; Gulka & Davoren, 2019). Seasonal variation in behavioural budgets were evident in the Gulf, reflecting shifts in oceanographic conditions and subsequent primary productivity and prey availability (Chang *et al.*, 2003; Piatt *et al.*, 2007). A decrease in foraging activity was observed in autumn, reflecting seasonal shifts in prey availability. Early spring through late summer in the Gulf is associated with strong stratification which drives seasonal upwelling and winter mixing. Subsequent plankton blooms and successive shifts in secondary producers leads to prey availability for predators at higher trophic levels (Chang *et al.*, 2003). Low autumn foraging may further reflect the changes in ocean conditions following autumnal storm events, which may alter the distribution and behaviour of prey (Fandel *et al.*, 2020). Likewise, late-summer marine heatwave events lower prey availability and quality, with bottom-up effects on planktivores' foraging behaviours, with poor foraging conditions forcing planktivores to exert greater foraging effort to maintain body condition (Evans *et al.*, 2021; Fromant *et al.*, 2021). We see a shift in Bryde's whales and common dolphins in warmer years (Colbert, 2019), so this may also hold for

some of the seabird taxa in the Gulf. Flesh-footed shearwaters vary their time spent foraging; however, we found no significant differences between seasons. These seasonal variations may indicate shifting prey availability and fuelling up before their trans-equatorial migrations leaving New Zealand in autumn, migrating north towards more productive ocean regions during non-breeding seasons (Rayner *et al.*, 2011; Shaffer *et al.*, 2006). However, not all of the Gulf's seabirds migrate and none of the cetaceans are migratory, and thus many species act as indicators of ecosystem changes in the Gulf year-round.

Intrinsic drivers of seasonal variation

Species-specific seasonal differences further reflect energetic requirements, including gaining energetic reserves for upcoming breeding seasons, offspring provisioning and preparation for long-distance migrations (Alerstam & Bäckman, 2018; Baert *et al.*, 2021; Collins *et al.*, 2016; Russell *et al.*, 2015). Seasonal differences in behavioural budgets reflect seasonal migrations of MSFA attendees, with behavioural plasticity buffering the effects of increased competition with arriving migrants, shifting prey availability and energetic constraints of breeding (Ismar *et al.*, 2011; Litzow & Piatt, 2003; Markones *et al.*, 2010). However, not all species' activity budgets were affected by season. Fluttering shearwaters did not show significant differences in the proportion of time spent in each behavioural state. This may be due to flexible foraging, with fluttering shearwaters foraging close to the coast, foraging further during non-breeding and pre-laying periods, suggesting release from constraints associated with central place foraging (Berg *et al.*, 2019). These obligate central place foragers likely change their behaviour to increase foraging efficiency, with coordinated parenting and flexible foraging allowing them to overcome foraging associated constraints (Boyd *et al.*, 2017; Burke & Montevicchi, 2009; Gillies *et al.*, 2021). Furthermore, we recognise that foraging may be constrained during the breeding season for central-place foraging seabirds, with incubation trips likely having different activity budgets to non-incubation or non-rearing times (Patenaude-Monette *et al.*, 2014; Ropert-Coudert *et al.*, 2004). In this study, we do not account for breeding differences; however, the seasonal differences in foraging likely reflect the increased energetic demands associated with reproduction and offspring-care (Fury *et al.*, 2013; Markones *et al.*, 2010). Seasonal behaviours of common dolphins indicated that they spent more time foraging in winter and spring. This finding is supported by earlier studies (Neumann, 2001; Stockin *et al.*, 2009), which suggest that seasonal fluctuations in primary productivity and prey drive the observed heightened foraging in spring. Common dolphin foraging is not limited by central-place breeding behaviours like many seabirds. However, activity budgets and foraging behaviours, including their position in MSFAs, are limited by constraints imposed when foraging with calves (De La Brosse, 2010). Bryde's whales did not show seasonal variation in the proportion of time foraging; however, reproductive limitations (i.e., calf care, lactation) may be attributed to fine-scale foraging variation not detected here. The Gulf is an important breeding ground for Bryde's whales, with high numbers of mother-calf pairings observed during autumn when MSFA participants tended to spend less time foraging (Wiseman *et al.*, 2011).

3.4.4 Clusters

Foraging niche partitioning allows similar species to co-exist and forage within MSFAs, with overlapping resource use and co-existence facilitated through differences in foraging behaviours and prey specificity. Foraging at different trophic levels within multi-trophic MSFAs (e.g., Cluster h) facilitates co-existence and minimises competition between predators with similar foraging ecologies (Merkle *et al.*, 2017; Perkins *et al.*, 2020). Behavioural differences by clusters highlight how large pelagic predators will show spatial and temporal foraging partitioning, targeting different prey to avoid competition (Varghese *et al.*, 2014). Clusters primarily composed of fish-feeding species spent more time engaging in active non-foraging and non-active non-foraging behaviours than planktivore clusters. With many predators foraging for the same prey, more time is spent counteracting the effects of heterospecifics than foraging, e.g., dolphins must herd prey to offset the vertical scattering effect of diving gannets (Vaughn *et al.*, 2008). While cluster was an important factor influencing foraging and non-active non-foraging, no significant differences between cluster pairs were found. Below we discuss the role of piscivores and planktivores using examples from this study.

Piscivores

Piscivore MSFAs were characterised by the attendance of fish feeding common dolphins and gannets. Common dolphins were important facilitators of MSFA events, with shared prey herding likely reducing the energetic costs of foraging compared to solitary foraging. The Gulf's dolphins often spend more time foraging in larger groups, with foraging being the most frequently observed behavioural state of common dolphins in the Gulf (Burgess, 2006; Stockin *et al.*, 2009). We also observed gannets spending large portions of time active non-foraging, circling the MSFA before diving, changing their dive height and angle depending on prey distribution and the presence of other predators (Machovsky-Capuska *et al.*, 2011b; Purvin, 2015).

Planktivores:

In contrast, plankton-feeders, including white-fronted terns, Buller's and fluttering shearwaters and storm-petrels, spent most of their time in MSFAs foraging. We expect these findings to hold for common diving petrels (*Pelecanoides urinatrix*; excluded from species analysis due to low attendance, Table 2.1), for whom foraging accounts for two-thirds of all behavioural states during their at-sea foraging activities (Zhang *et al.*, 2019). Unlike fish-feeders, planktivores are surface feeders and shallow divers, with foraging depth limited by prey availability. The increased time spent foraging by planktivores suggests active pursuit diving may be more costly than surface plucking (Ballance *et al.*, 1997; Croxall & Prince, 1980; Dänhardt & Becker, 2011). We saw non-diving seabirds spending longer actively foraging than those engaging in costly behaviours such as plunge dives, pursuit dives and take offs (Collins *et al.*, 2016). These smaller planktivorous seabirds have lower flight costs in proportion to body size, thus allowing them to spend more time flying and foraging and less time resting and recovering (Ballance *et al.*, 1997). Low flight costs are associated with increased dependence on aerial feeding techniques such as dipping and surface seizing, which allow them to

capture prey and quickly take-off or remain in flight while foraging (Croxall & Prince, 1980; Shealer, 2002).

Terns, shearwaters, and storm petrels were observed surface plucking, relying on subsurface predators, including kahawai (*Arripis trutta*) and trevally (*Pseudocaranx dentex*), to herd prey to the surface for easier access (Frost, 2017; Michel *et al.*, 2022). This small-scale vertical shift in prey distribution increases prey accessibility and removes constraints associated with prey depth distribution. However, foraging alongside predatory fish may come at a cost. The presence of fish prey within the MSFA attracts fish-eating and kleptoparasiting predators, excluding planktivorous seabirds from the core of MSFAs. Collision, prey-stealing and predation risk drives smaller, less gregarious species to remain at the periphery and spend less time foraging (Beauchamp, 2012; Hoffman *et al.*, 1981; Machovsky-Capuska *et al.*, 2011a). White-fronted terns were not often seen resting (non-active non-foraging). This may be in response to perceived vulnerability to predation by the subsurface predators they are foraging alongside (Duffy & Taylor, 2015; Meyer *et al.*, 2010; Ulman *et al.*, 2015). When exposed to perceived and actual predation risk, we expect activity budgets to shift from active foraging to active non-foraging behaviours.

3.4.5 Next steps and concluding remarks

This study provides new information on the factors influencing behavioural activity budgets of species within MSFAs in the Gulf. While previous studies have provided an overview of presence-absence patterns of species, this study has investigated factors affecting species behavioural budgets during MSFA events. It has also provided insights on the potential effects of prey type and species co-occurrence. Predator activity budgets give indices on prey availability, allowing them to be used as assessment tools for fluctuating foraging conditions, particularly in response to changes in ecosystem health.

This chapter presents a general overview of the proportion of time groups spent in the various behavioural states during MSFA events. Due to the nature of this overview, we were not able to investigate patterns of behaviours, instead presenting a general overview of the behaviours we see during the MSFA events. Our behavioural observations have noted key patterns that would be interesting to analyse in future studies or re-analysis of the raw data. Phases of MSFA events would further provide valuable insights into the role of species in MSFAs. For example, as reported previously (Gostischa *et al.*, 2021; Purvin, 2015; Wiseman, 2008), Bryde's whales had a scattering effect on MSFAs acting as a terminator in particular when lunge feeding on fish, drastically reducing prey availability for other species. This prey minimisation and scattering led to reduced foraging activity, with MSFA participants shifting from active foraging to non-active behaviours such as milling, slow travel and resting. Following the scattering and dispersal of prey, resting and rafting (non-active non-foraging) increased towards the end of MSFAs, highlighting that searching for prey is not

profitable once the prey patch has been scattered or depleted (Sparling *et al.*, 2007; Thums *et al.*, 2013).

Our study also evidences the magnitude of data required for analysing and understanding behavioural budgets for individual species foraging within MSFAs. Due to the seasonal attendance of migratory species, sufficient temporal spread of survey effort is required to avoid data gaps for migrant species. With the incorporation of new techniques, such as telemetry and drone videography, we will be able to conduct fine-scale analysis of movement and foraging data. Drones have already proved useful in enhancing behavioural studies of cetaceans in the Gulf, enabling the recording of behaviours to greater accuracy than just boat-based surveys (Fettermann *et al.*, 2022; Izadi *et al.*, 2022). By incorporating the behaviours of sub-surface prey and species better observed from air, such as sharks and rays (Hamilton, 2020), future studies would also be able to better understand the relationships between species that forage together near the sea surface.

Activity budgets and the ways species forage and interact within MSFAs can be valuable indicators of ecosystem health. Animal behaviour is thus important for the continued monitoring of marine predators in the Gulf, with behavioural data providing insights into the intricate communities that aggregate at ephemeral and patchily distributed prey. With changing ocean conditions, climate change and prey availability and abundance, we expect these behavioural budgets to shift, highlighting the need for continued monitoring of MSFA dynamics over time.

Chapter 4 Drones and Artificial Intelligence in Marine Ecology

4.1 Introduction

The marine environment is dynamic and vulnerable to threats, with reliable data needed to inform research, monitoring and conservation efforts. The Gulf is a highly productive environment that attracts and hosts a wide range of marine predators, ranging from small New Zealand and white-fronted storm petrels (*Fregetta maoriana* and *Pelagodroma marina*) to 15 m long Bryde's whales (*Balaenoptera edeni brydei*) (Gaskin & Rayner, 2013; Gostischa *et al.*, 2021; Hamilton, 2020). These predators are key indicators of ecosystem health, with association patterns and diets reflecting shifts in prey availability and abundance (Carroll *et al.*, 2019; Gostischa *et al.*, 2021). Given the rapidly changing state of ocean health, remote surveying tools are beneficial for scientists, with animal behaviours and movement patterns acting as indicators of ecosystem health. As behavioural ecology has progressed, studies have shifted from descriptive observational records (Altmann, 1974; Altmann & Altmann, 2003) to using low-cost, field-deployable technologies, including remotely sensed imagery and computer science tools (Finn *et al.*, 2019; Hughey *et al.*, 2018; Nazir & Kaleem, 2021). Modern technology has become an essential component of ecological studies, enabling researchers to answer increasingly complex research questions and address global challenges (Allan *et al.*, 2018; Marvin *et al.*, 2016).

4.1.1 Drones in Marine Ecology

Increased accessibility and development of remote imaging tools have revolutionised monitoring and surveillance studies of near-surface-dwelling marine species (Bicknell *et al.*, 2016; Frouin-Mouy *et al.*, 2020; Schaub *et al.*, 2018). Advancements in unmanned aerial vehicles, hereafter referred to as drones, can enable wider spatial areas to be surveyed in more detail than planes whilst minimising human disturbance, producing high-quality footage that can be shared and analysed by multiple stakeholders and researchers, fostering research collaboration (Gallego & Sarasola, 2021; Jagielski *et al.*, 2022; Saunders *et al.*, 2022). Drones are a valuable platform for collecting behavioural data on elusive, cryptic or less abundant species, which are by nature challenging to observe in marine habitats (Corcoran *et al.*, 2021; Fettermann *et al.*, 2022; Griffin *et al.*, 2005; Schofield *et al.*, 2017; Torres *et al.*, 2018). Drone surveys provide platforms for assessing aspects of ecology, including shoaling patterns (Rieucau *et al.*, 2018), population densities (Kiszka *et al.*, 2016), mating behaviours (Bevan *et al.*, 2016; Schofield *et al.*, 2017) and social interactions (Fettermann *et al.*, 2022; Smith & Pinter-Wollman, 2021).

In the marine environment, animals that are nekton/surface dwellers lack continuous visibility from the surface, with only a fraction of their behaviours visible from surface platforms creating challenges

for behavioural ecologists (Nowacek *et al.*, 2016). Drones overcome these limitations by providing a 'birds-eye-view' of surface-dwelling predators, including elasmobranchs (Gallagher *et al.*, 2018; Kiszka *et al.*, 2016; Rieucan *et al.*, 2018), sea turtles (Bevan *et al.*, 2016), and marine mammals (Frouin-Mouy *et al.*, 2020; Landeo-Yauri *et al.*, 2020). Drones are gaining popularity as effective, portable methods of animal behaviour sampling, providing high-quality images. While many are equipped to collect high-resolution imagery, a critical limitation is the manual processing and visual detection tasks. The increased use of drones in ecology highlights the need for automated and assisted analysis tools to process large amounts of data.

4.1.2 Artificial intelligence in Marine Ecology

Artificial intelligence (AI) and machine learning (ML) tools are becoming increasingly available, accessible, and transferable, increasing the capacity for automated and assisted analysis of a wide range of datasets, complementing traditional analyses (Tabak *et al.*, 2020). By creating ML tools, manual processing can be reduced, allowing researchers to conduct high-throughput screening and analysis of large datasets with greater sensitivity and accuracy (Borowiec *et al.*, 2021; Peters *et al.*, 2014; Tuia *et al.*, 2022). The information generated using ML tools can be used to infer and quantify various information on organisms that are hard to observe directly, such as seabirds (Carroll *et al.*, 2014; Korpela *et al.*, 2020), marine mammals (Blount *et al.*, 2019; Durban *et al.*, 2016; Ladds *et al.*, 2016) and elasmobranchs (Brewster *et al.*, 2018; Johnson *et al.*, 2017; Whitehead *et al.*, 2021; Whitehead *et al.*, 2017).

ML tools have bloomed as a tool in ecological studies and wildlife monitoring programmes, providing novel insights into the ecology of cryptic and hard to monitor species (Gemert *et al.*, 2014; Gonzalez *et al.*, 2016; Setyawan *et al.*, 2022). Developing ML tools enables us to create predictive models that can accurately achieve a task with high precision on previously unseen data. Such tasks include classifying species and animal behaviour from imagery (Aguzzi *et al.*, 2009; Kabra *et al.*, 2013; Nguyen *et al.*, 2017; Siddiqui *et al.*, 2018; Wäldchen & Mäder, 2018). Convolutional neural networks (hereafter CNN) frequently use deep learning architectures with multi-layered machine learning units to identify features of various weightings in data to classify and identify objects (Gu *et al.*, 2018). The development of CNNs has allowed researchers to overcome difficulties associated with analysing large imagery data sets, such as those collected by drones. CNNs can be developed to automate the detection of specific features and objects, such as animals, from large images and videos with human-like accuracy (Maire *et al.*, 2014; Mardiyah & Purwaningsih, 2020; Nguyen *et al.*, 2017). CNNs have contributed significantly in furthering our understanding of marine species dynamics, such as classifying plankton (Rawat *et al.*, 2019) and coral species (Sharan *et al.*, 2021) and detecting large marine animals from drone footage (Boudaoud *et al.*, 2019; Butcher *et al.*, 2021; Gray *et al.*, 2019a; Gray *et al.*, 2019b)

Classification of different species and behaviours using CNNs is robust and allows for the assessment and analysis/discrimination of features at different scales and species levels. Combining UAVs and CNNs creates the opportunity to build scalable systems. The addition of new species and background contexts offers the potential to upscale, collate, and apply these analyses to other studies and environmental and behavioural contexts (Olson *et al.*, 2018). With improved image quality, CNNs can define and detect specific points of interest with increasing detail, accuracy, and flexibility, highlighting the need for further investment in this area (Borel-Donohue & Young, 2019).

In this proof-of-concept study, a CNN was developed to determine whether ML can be used to automatically detect seabirds and cetaceans, and their behaviours from drone imagery. We generated a species diverse visual dataset to develop a CNN by flying small commercially available drones above individuals and groups of various species. Here, we create a pipeline for analysing imagery collected via drone, integrating image annotations, enhancement, and augmentation to define, train and validate data sets using machine and deep learning tools. This study reflects on the practicality and generalisability of CNN development in animal behaviour studies, particularly for analysing drone imagery of marine animals.

4.2 Methodology

4.2.1 Study areas

Drone footage was collected during research trips on the *RV Hawere*. See Chapter 2.2 Methodology for details regarding research trips.

4.2.2 Drone footage collection

Drones were used to collect high-definition video footage of both single species groups and multi-species foraging associations (MSFA), providing a 'birds-eye view' of above and sub-surface predators and their foraging behaviours at the air-sea interface. All drone footage was captured using the commercially available quadcopter, DJI Mavic 2 Pro (for full camera specs, see: <http://www.dji.com/nz/mavic-2>), equipped with a 4k (3840 x 2160, 30fps) resolution camera with 48° to 83° field of view and a UV filter fitted to the lens. Its lightweight and portable design allowed easy transport and take off from the research vessel without a dedicated launch platform. The drone team consisted of a pilot who flew the drone and visual observers who recorded boat-based observations (see Chapter 2 section 2.2 and Chapter 3 section 3.2 for boat-based observation methodology) and assisted the pilot in locating the MSFAs and areas for targeted filming. Observers were present during flights to assist in keeping visual contact with the drone and direct the pilot towards the MSFAs due to the ephemeral nature of MSFA events and movements of marine predators.

Flight protocol

The drone was piloted using the DJI smart controller, which provided a live video stream, allowing the pilot to collect appropriate imagery. Live streaming assisted the pilot in positioning the drone above objects of interest, in our case seabirds and cetaceans, to collect representative and targeted footage for use in CNN development. Where possible, less frequent attenders, such as Bryde's whales, were followed to collect sufficient data. For each drone flight, it was launched from the bow of the research vessel and then flown towards the animals, maintaining an altitude above that of the highest-flying seabird (20 - 50m - following permitted protocols by the Department of Conservation - Te Papa Atawhai and University of Auckland - Waipapa Taumata Rau Animal Ethics Committee to Rochelle Constantine). The drone was flown ~30m above the animals of interest, with the camera pointed directly down at a 90° angle. The camera angle was adjusted periodically to position, follow, and find the animals but returned to 90° to continue collecting footage. The drone can withstand wind speeds up to 29-38kph and provides flight and hover times of ~30 minutes. Low battery power, strong wind or cessation of the foraging behaviours led to retrieval of the drone.

4.2.3 Machine learning training and testing

We developed a CNN to automatically process drone footage to determine whether automated analysis of visual data would be feasible in future research. Our method used an object detector (YoloV4, Bochkovskiy *et al.*, 2020) to pull specific animals out of the video and a second stage classifier to train a single species classifier (ResNet-50; He *et al.*, 2016). By analysing individual pixels, the classifier tool can automatically assign collections of pixels above or below a threshold to a classifier – this works particularly well for animals with high contrast to the background (Gonzalez *et al.*, 2016).

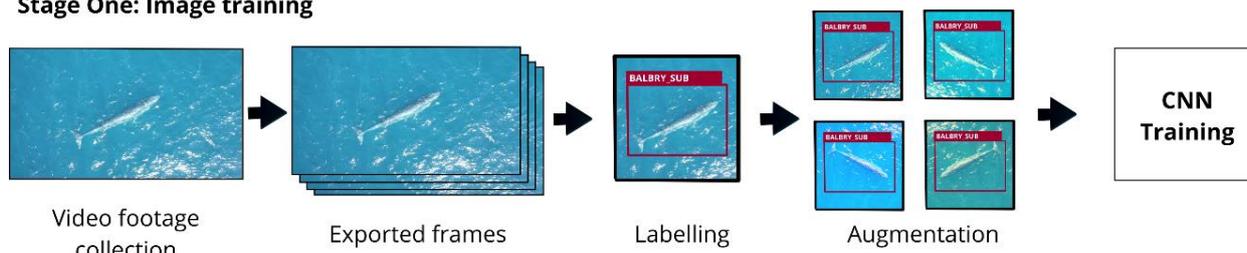
Table 4.1 Artificial Intelligence terminology and definitions

AI Terminology	Definition
Objects	One or more effective targets from still images or video data – i.e., an animal in the frame.
Images	A visual representation of a collection of pixels may be whole or part of original images. Higher resolution images have a greater number of pixels.
Annotations	Labelled data tailored to the dataset which show the outcome we want the CNN to detect. In images, annotations may be bounding boxes on images containing targeted objects
Bounding boxes	Co-ordinates which serve as a point of reference for object detection outlining objects of interest within an image using X-Y coordinates.
Augmentation	Artificial generation of training data from annotated data. New training data feeds a greater variety of data to the model, increasing its accuracy under different conditions and scenarios.
Batch	The number of training samples/data in one iteration.
Iteration	One-time processing for a batch of images. The number of batches.
Epoch	A full cycle of the training of the CNN with the full training data.
Layers	Non-linear stepwise operations within a CNN. Each layer transforms the last, extracting features to learn image features. The output layer transforms these into a fully connected layer with detected objects and classes as trained by the model.
Recall	The measure of the CNN correctly identifying true positives, out of all the actual number of positives.
Precision	The ratio of true positives to the total number of positives.
Loss	Prediction error of the CNN.
Accuracy	Performance of the CNN comparing the precision (correct results) with recall (correct answers) of the model predictions compared to the training dataset.

Image processing

Drone image collection was followed by a labelling and training process (Figure 4.1, stage one). First, drone video quality was determined by focus, contrast, brightness, and glare then scored from excellent to poor using the assessment criteria (Table 4.1). From suitable 4K, perpendicular video footage, every fourth frame was extracted into a jpeg format. Imagery that was overexposed, blurred, or not approximately 90° was omitted from tagging. This filtering and sorting ensured that trained imagery had sufficient resolution and desirable angles and altitude for object characteristics to remain relatively consistent for CNN training. The images were manually processed and annotated, with the animals and their behavioural states labelled with unique classifiers (Table 4.2).

Stage One: Image training



Stage Two: Image Testing Process

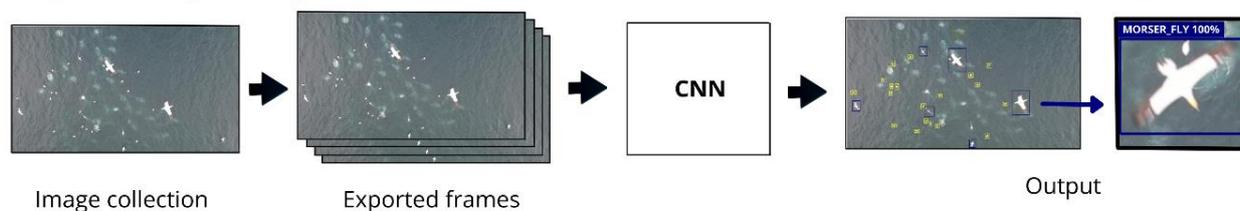


Figure 4.1 Stages involved in the training of the convolutional neural network (CNN) to detect target animals and behaviours from drone footage. *Stage One:* Collect and extract images from drone footage, labelling inputs with classifiers and augmenting the inputs to train the CNN. *Stage two:* Training and validating the CNN using training and validation datasets.

Table 4.2 Grading system (1 - 4) and assessment criteria to evaluate drone image quality.

	Examples		Assessment criteria
Excellent (1)			Sharp focus, clear contrast, and minimal sun glare. Observers can distinguish detail in sub-surface predators.
Good (2)			Sharp focus, clear contrast, some sun glare. Visibility extends through the water column, and animals below the surface are distinguishable
Okay (3)			Sun glare, turbid water/low contrast due to overcast/clouds. Visibility is restricted to the top few meters of the water column.
Poor (4)			Poor contrast (turbid or overexposed) and moderate sun glare. Visibility is highly restricted on/near-surface.

Image processing and annotations were carried out using the open-source graphical user interface (GUI) YOLOLabel v1.1.1 (https://github.com/developer0hye/Yolo_Label; Figure 4.2). Using this GUI, 15,912 images were manually annotated using 119,950 bounding boxes (pixel coordinates) labelled with unique classifiers indicating the animal and its behaviour (Table 4.3). Images were fully annotated to avoid automatically assigning non-annotated pixels containing species to 'background', with trained bounding boxes operating only on the cropped regions around the objects of interest (Norouzzadeh *et al.*, 2021). During CNN training, ~90% of the annotations were used to train the model, and the remaining ~10% were used to test the model. This 90-10 ratio is standard practice for AI model development, reducing human bias when testing the model (Goodfellow *et al.*, 2016; Mardiyah & Purwaningsih, 2020). Due to limitations in available imagery, only the following species were used to train the CNN; common dolphins (*Delphinus delphis*), Bryde's whales, Australasian gannets (*Morus serrator*), white-fronted terns (*Sterna striata*), fluttering (*Puffinus gavia*), Buller's (*Ardenna bulleri*), flesh-footed (*Ardenna carneipes*), and sooty shearwaters *Ardenna griseus*).

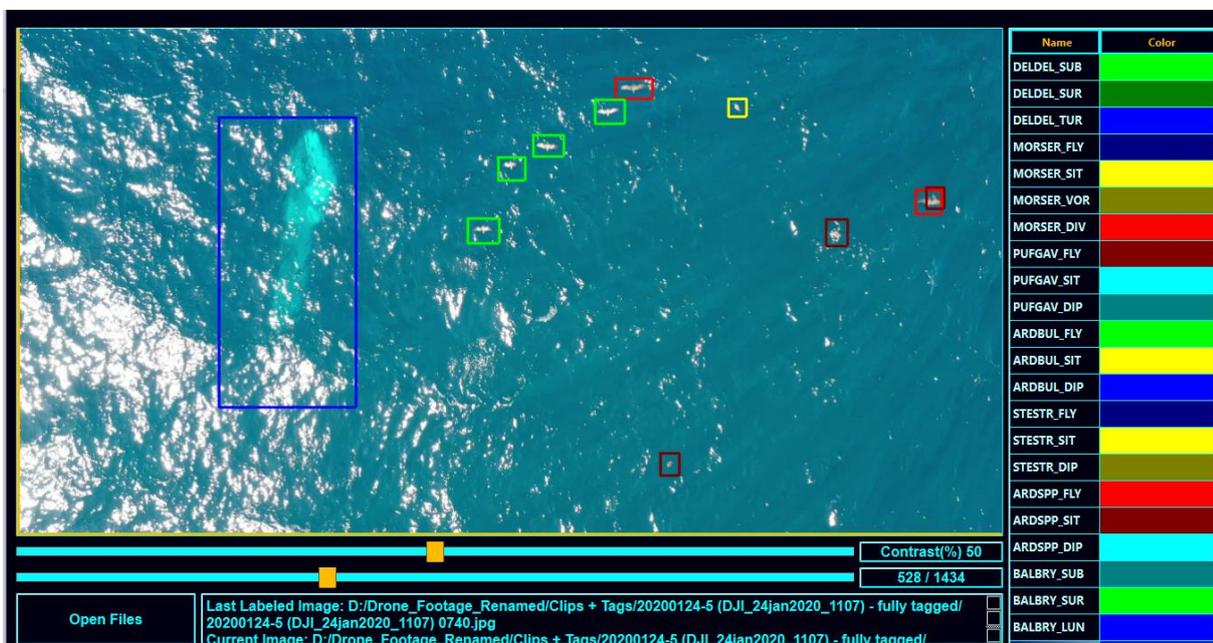


Figure 4.2 Example of YoloLabel graphical user interface with bounding boxes and associated species and behaviour classifiers listed. Bounding boxes are generated by the annotator with colours used as a visual aid to help distinguish between the different classifiers

A minimum of 2000 bounding boxes were drawn per class to balance the training dataset. Classifiers that were difficult to detect or had below 2000 images were excluded from final model development (Table 4.3). Animal behaviours were determined by following the animals and comparing frames, with movement and colour patterns aiding species identification and behaviour classification. Due to morphological similarities between flesh-footed and sooty shearwaters, images of these birds were combined to form the group 'ARDSPP' (*Ardenna spp.*)

Table 4.3 Seabird and cetacean CNN classifiers and behavioural descriptions. See the glossary for the scientific names of each of the species. Excluded refers to classifiers which did not meet the 2000 image criteria for inclusion.

Single-species classifier	Behaviour Classifier	Behaviour	Description
Buller's shearwater ARDBUL	ARDBUL_FLY	Flying	Both wings extended. Dark 'M' pattern across the wings.
	ARDBUL_SIT	Sitting	Large dark bird, easily recognisable from prior flying.
	ARDBUL_DIP	Dipping	EXCLUDED
Ardenna spp. ARDSPP	ARDSPP_FLY	Flying	Large dark brown bird, wings extended
	ARDSPP_SIT	Sitting	Dark brown, large bird sitting.
	ARDSPP_DIP	Dipping	EXCLUDED
Bryde's whale BALBRY	BALBRY_SUB	Sub-surface	Clearly visible with no body parts above the water, belly downwards.
	BALBRY_SUR	Surfacing	At the surface, various body parts disrupting the surface. Includes exhalant blows
	BALBRY_LUN	Lunging	Side on position with ventral pleats (mouth) visible. Includes pre, during and post gulp positions.
Common dolphin DELDEL	DELDEL_SUB	Sub-surface	Clearly visible with no body parts above the water, belly downwards
	DELDEL_SUR	Surfacing	Various body parts disrupting the surface.
	DELDEL_TUR	Turning	Body is turned into a 'C' or banana shape, indicating a tight turn. Associated with herding prey.
Australasian Gannet MORSER	MORSER_FLY	Flying	Outstretched wings with black tips on wings and tail and yellow head.
	MORSER_SIT	Sitting	Bright white, large seabird with a teardrop shape and black tail
	MORSER_DIV	Diving	Tight wings, bullet shape. Includes movement pre and during dive.
	MORSER_VOR	Vortexing/ bubbles	Bubble trail from dives, tracing its trajectory
Fluttering shearwater PUFGAV	PUFGAV_FLY	Flying	Both wings outstretched, often blurred due to rapid wing movement.
	PUFGAV_SIT	Sitting	Small brown bird sitting on the surface. Teardrop shape
	PUFGAV_DIP	Dipping	EXCLUDED
White-fronted tern STESTR	STESTR_FLY	Flying	Small white bird with wings outstretched, forked tail
	STESTR_SIT	Sitting	EXCLUDED
	STESTR_DIP	Dipping	EXCLUDED

Behaviour descriptors and classifiers are distinguishable through basic object attributes such as body colour and colour patterns, body shape in different states (i.e., sitting with wings tucked in vs flying with wings outstretched), and size relative to other objects in the frame (Figure 4.3).

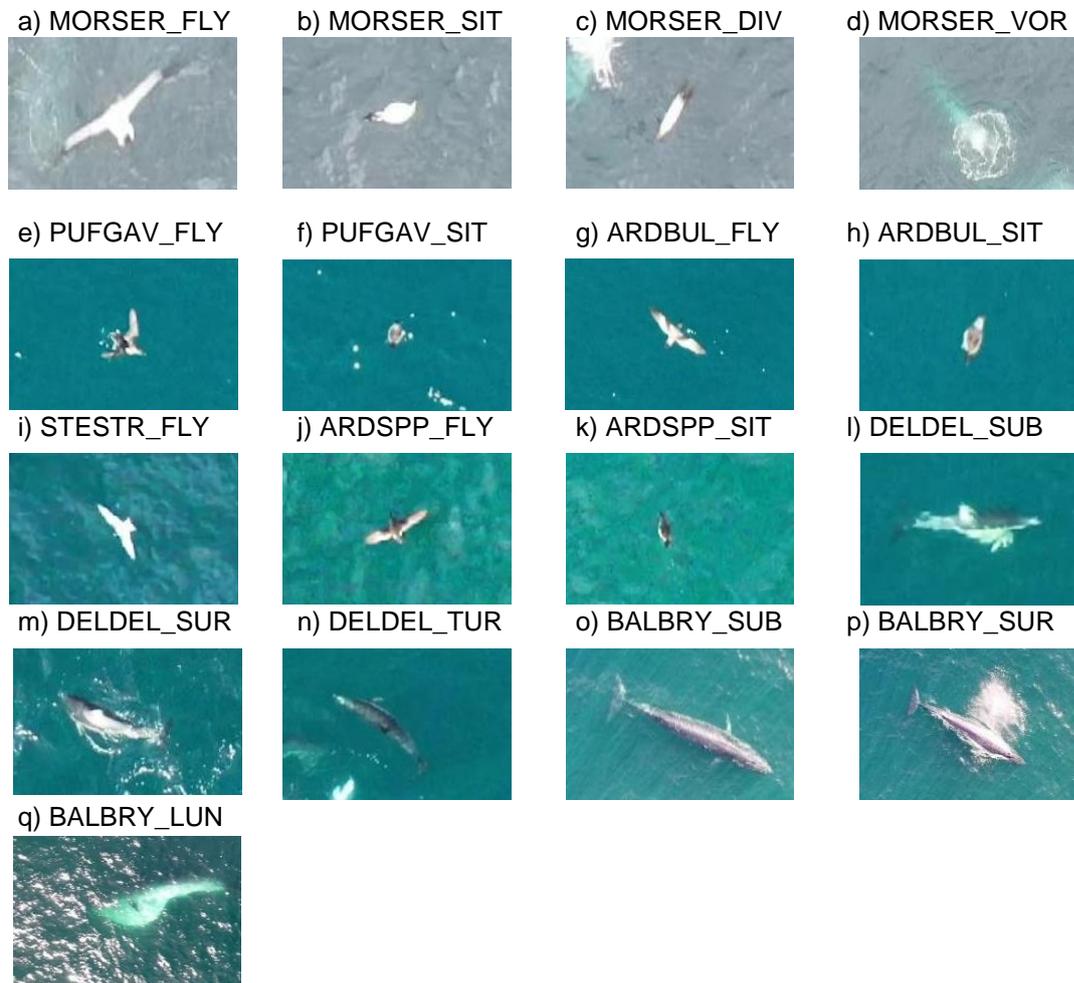


Figure 4.3 Examples of still images captured from drone imagery illustrating the 17 behaviour classifiers used in CNN training (see table 4.3 for descriptions). Images a-d illustrate Australasian gannet (MORSER), e and f fluttering shearwaters (PUGGAV), g and h Buller’s shearwaters (ARDBUL), i white-fronted terns (STESTR), j and k *Ardenna* spp. (ARDSPP), l-n common dolphins (DELDEL), and o-q Bryde’s whales (BALBRY).

Stage three: Image pre-processing

The third stage of this study was to pre-process the images to increase variation, contrast, background, and textures. Image augmentation, such as cropping and rotation, further increased the training image pool by artificially obtaining more images (Goodfellow *et al.*, 2016; Shorten & Khoshgoftaar, 2019). Augmentation processes were applied programmatically and randomly throughout the training process.

Data augmentation and management were conducted using python using the libraries ‘numpy’ (C. Harris *et al.*, 2020), ‘pillow’ (Clark, 2015), ‘opencv’ (Bradski, 2000), and ‘pandas’ (McKinney, 2010,

2011). Augmentation was achieved through distortion and image occlusion using ‘darkmark’ (<https://www.ccoderun.ca/darkmark/DataAugmentationColour.html>).

The resulting augmented images created new data from existing manually processed imagery, increasing the size and variation of the dataset. Photometric distortion by changing the brightness, contrast, saturation, and noise of images improves the model’s performance in different oceanic conditions, time of day, and camera/drone use. Due to the nature of the drone data and presence of submerged and partially submerged animals, we did not apply ‘mosaic’ (Hao & Zhili, 2020) or ‘cutmix’ (Walawalkar *et al.*, 2020) augmentations as resultant images do not look like our targeted animals and thus decrease object detection performance. Using augmentation, we aimed to increase the data to build a robust model capable of detecting objects under a range of conditions and scenarios (Bochkovskiy *et al.*, 2020).

Table 4.4 Augmentations applied to this model.

Augmentation Technique	Definition/Process
Photometric distortion	Changing the brightness, contrast. Saturation and noise of an image. In this model the following photometric distortions were applied: saturation - 1.5, exposure - 1.5, and hue - 0.1.
Geometric distortion	Scaling, cropping, flipping, and rotating objects to create variations of the data to generalise the model.
Letterbox	Generalises the dataset by ensuring the image x-y ratio is consistent.
Random erase	Replacement of regions of the image with random pixels preventing the model from memorising specific pixel values, reducing the probability of overfitting the model to the training dataset.
Hide and seek	Hides patches of the image slowing the model to learn different portions of the object.
Grid mask	Regions of the image are hidden, forcing the model to learn specific components of individual objects.
Random erase	Randomly erases sections of images simulating scenarios where objects are not fully visible.

Stage four: Machine learning training

The fourth and final step was to train the CNN for object recognition and classification. CNNs perform sequences of operations, called layers, with each layer processing the previous layer's output until the final layer can be classified as a particular object. For a technical overview of CNN development and processing, see LeCun *et al.*, (2015). Throughout the training, we held a batch size of 64 with four subdivisions, ensuring the model was seeing all the data every four iterations.

We trained our model using the following hardware: AMD Ryzen Threadripper 3970x 32 core 64 thread CPU, 256gb Memory, 2 x Nvidia RTX A6000 GPU with 48gb memory each (NVLINK), and 2 x NVME 2TB PCIe 4.0 SSD.

As neural network modelling is computationally intensive, hardware specialisations are needed to improve model performance (Schmidhuber, 2015). The upgraded GPU capacities allowed us to use higher resolution imagery for training and testing the model. We aimed to generate 10,000 images per animal during image training, with 2000 per class to build a robust model. This is seen as the minimum for a robust computer vision model with pre-augmentations being applied (Bochkovskiy *et al.*, 2020), as proven in the detection of Māui dolphins (*Cephalorhynchus hectori maui*) by MAUI63 (<https://www.maui63.org>; van der Boon, pers. comm.).

In this study, we used two different CNNs. Our first model used YoloV4 (C & C++; <https://github.com/AlexeyAB/darknet>) to detect and extract images containing objects of interest (Table 4.3) from imagery. Early model testing found greater accuracy with increased image resolution (pixels) than increased layers in the CNN (See Appendix 2-4 for model performance at various training intervals). Initial model training identified objects at a behaviour level. To improve on the capacity of the model to detect species, we used the training data to form a second stage classifier model, whereby the model first identified the species, then the behaviour it is engaging in.

This second CNN used a ResNet-50 network that is 50 layers deep (48 Convolution layers along with one MaxPool and one Average Pool layer) to analyse cropped images (224 x 224 pixel resolution) and classify animals and their behaviours with higher accuracy using a two-step system. The first step of the ResNet-50 system identified the species (Table 4.3). ResNet-50 combined with the Nvidia TAO tool kit (<https://docs.nvidia.com/tao/tao-toolkit/text/overview.html>) and Tensorflow (Citro *et al.*, 2015; https://www.tensorflow.org/api_docs/python/tf/keras/applications/resnet50/ResNet50), were used to enhance classification through transfer learning. Transfer learning was facilitated by using the Transfer Learning Toolkit in the Nvidia Tao toolkit. This transfer toolkit was then trained on a subset of the Google Open Images dataset and gave the model a base to learn, saving training time. ResNet-50 was chosen due to its accuracy and the small amount of training time required. Our final model with single animal-classifier detector ran at 29 layers with a resolution 2016x1152 pixels,

identifying six single species classifiers ARDBUL, ARDSPP, BALBRY, DELDEL, MORSER, and PUGGAV (Table 4.3). The second step of the ResNet-50 CNN will be to train the CNN to identify the behaviours (Table 4.3) of the animals it detects and classifies. This second step is part of future research and is currently in development and, as such, is not included in this thesis.

Machine learning assisted tagging

Once the preliminary CNN model was developed, we used it to accelerate the tagging process. This user-driven process involved feeding untrained images into the CNN, which were then tagged with predicted bounding boxes with associated classifiers. Due to the low accuracy of the preliminary model, corrections to these auto-tagged batches were needed. This step also allowed for mispredictions to be visualised, identifying potential confusion points in the model. Auto tagged and corrected objects were compared, giving a ‘corrected’ number of objects per video clip.

4.2.4 Data analysis and evaluation metrics

We tested our model's performance using the Mean Average Precision of the object detector based on precision-recall curves (Henderson & Ferrari, 2016). Using the testing data set (10% of manual tags), images were fed to the CNN model and tagged with bounding boxes – these CNN predicted bounding boxes were then compared to the manually annotated bounding boxes. A bounding box predicted by the CNN is treated as a true positive if the predicted bounding box overlaps the ground truth (manually annotated) bounding box (Intercept Over Union (IoU), Table 4.4) by at least 50% and has been predicted with the correct classifier. The IoU score ranges from 0 (no overlap) to 1 (complete overlap), with 0.5 being considered a true positive.

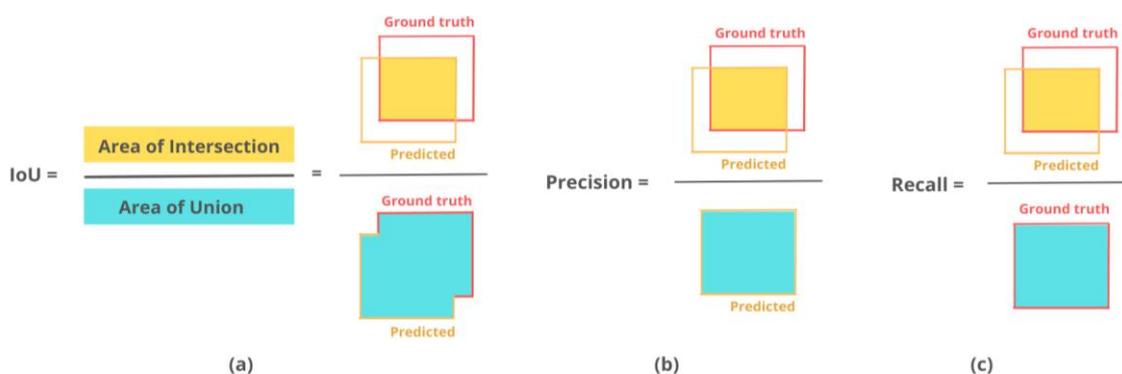


Figure 4.4 Geometrical representations of (a) IOU, (b) precision and (c) recall. Adapted from <https://github.com/AlexeyAB/darknet>.

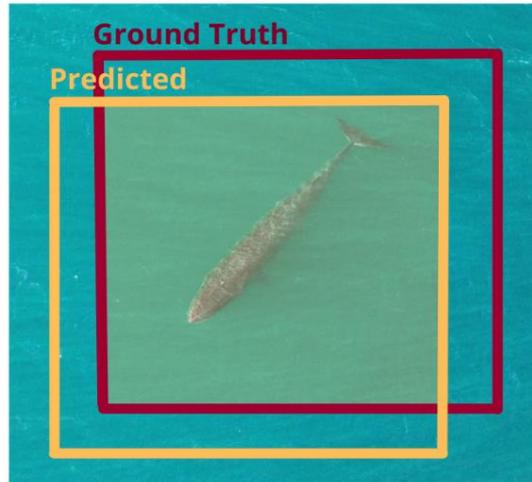


Figure 4.5 Example of true positive detection (>50% Intercept Over Union) from drone image showing ground truth (manual bounding box, red) and predicted (yellow) bounding boxes (areas of union) with the area of overlap (intercept, yellow) shaded.

The model's performance was evaluated using mAP (mean average precision, Equation 4.2). Average precision (AP, Equation 4.1) summarises the precision-recall ratio curve, with precision being the ratio of true positives to the total positives and recall, the ratio of true positives compared to all positives. The higher the IoU requirement, the more precise the model (Rahman & Wang, 2016; Rezatofghi *et al.*, 2019) – for this model, an IoU of 50% was used as a measure of ‘true positive’. Average precision can then be used to generate the mean average precision (Equation 4.2).

Equation 4.1 Average Precision (AP)

$$AP = \frac{Precision}{Recall} = \frac{\left(\frac{True\ Positive}{True\ Positive + False\ Positive}\right)}{\left(\frac{True\ Positive}{True\ Positive + False\ Negative}\right)}$$

Equation 4.2 Mean Average Precision (mAP)

$$mAP = \frac{\sum_{q=1}^n AP(q)}{n}$$

When calculating mAP, n is the number of queries in a set, and q is the given query.

For a given query, q, we calculate AP, and the mean gives us the mAP.

4.3 Results

From September 2019 to August 2021, a Mavic 2 Pro drone was deployed from the *RV Hawere* on one or more occasions during 19 of the 45 research trips to collect imagery of MSFAs. Once the pilot located the target animals, they flew above the group at a constant altitude of ~30 m to record a representative example of different behaviours. A total of 51 drone flights were undertaken, during which 14hr 7 mins (average \pm SD; 14.85 ± 8.74 min) of footage were recorded from leaving the boat to returning. Once the pilot located the animals of interest, 246 videos ranging from 0.02 – 13.78 min were collected with an average (\pm SE) duration of 3.14 ± 0.13 min per video. Almost half (48%; $n = 117$) of the 259 video clips were centred above active MSFA events; the remaining 55% ($n = 129$) followed groups or individuals of single species foraging, travelling, and sitting/resting. Of these clips, 28 were selected for AI training; these videos featured animals for which classifiers were being trained, were high quality (Table 4.2) and were filmed at a 90° camera angle. As training progressed, video clips featuring specific species and behaviours were selected to reach the 2000 - 10,000 image requirement for CNN development and classifier training (Table 4.3).

For each video clip, every fourth frame was extracted to form our imagery dataset. Unsuitable images (i.e., poor quality, angle and/or blurred) were removed from the data set, resulting in 25,963 usable frames (average \pm SE; 927 ± 121 , range 107 – 2111 per video). From those frames that included one or more animals engaged in one or more behaviours, 166,040 (average \pm SE; 5930 ± 1548 , range 174 – 30,431 per video) annotations were generated using a combination of manual and assisted tagging.

4.3.1 Model misidentifications

During the correction of automatically tagged classifiers, we noted misidentifications. For example, Bryde's whales' tails were occasionally classified as 'common dolphins' (Figure 4.6a) with the grey colouration and curved shape visually similar to that of dolphin classifiers. Large surface ripples were occasionally tagged as subsurface Bryde's whales (Figure 4.6b). Surface conditions were also attributed to the misclassification of Australasian gannets and white-fronted terns, whose white bodies were visually similar to surface splashes and glare (Figure 4.6c). White-fronted terns were sometimes mistaken for gannets due to their white colouration. The tern's forked tail and lack of black markings help distinguish the two species; however, these features are harder to discern when the birds are sitting. Floating matter also caused further misidentifications, with seaweed being identified as ARDSPP (*Ardenna spp.*), with its brown colour matching that of the sooty and flesh-footed shearwaters (Figure 4.6d). Unsurprisingly, CNN also mispredicted sitting brown birds, including Buller's, fluttering, and *Ardenna spp.*, which are visually similar and only distinguishable by relative size to each other.

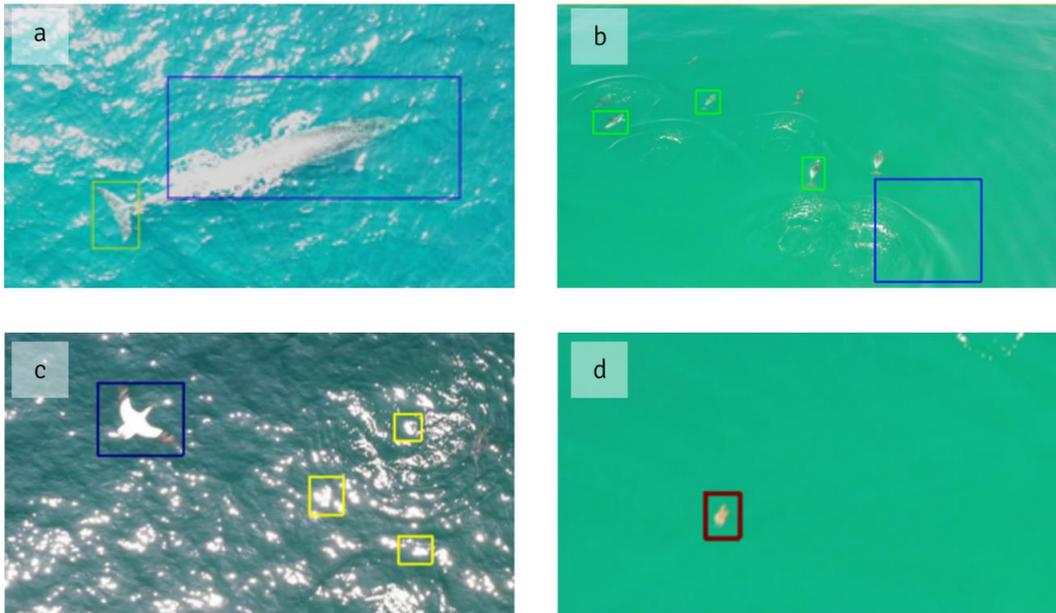


Figure 4.6 Examples of misidentified objects during auto-classification corrections. a) Bryde's whale (blue) tail misidentified as dolphin (yellow); b) surface ripple identified as Bryde's whale (blue); c) surface flare misidentified as sitting gannets (yellow); d) floating seaweed misidentified as *Ardenna* spp. - shearwaters (red).

Automated classification was applied to 10,051 images, with 28,198 tags automatically added and exported as bounding box coordinates. To fully correct the imagery, 17,892 annotations were added using the YOLO GUI, with fully trained images then used to train the next iteration of the CNN. The number of corrections per image (Figure 4.7) below showcases the corrected false negatives and positives. From these results, across all the video clips, we see Buller's shearwaters flying (ARDBUL_FLY) and common dolphins beneath the sea surface (DELDEL_SUB) required the highest number of additional tags per image (average corrections \pm SE; 0.33 ± 0.27 and 0.33 ± 0.32 respectively). Fluttering shearwaters flying (PUFGAV_FLY) and sitting (PUFGAV_SIT) had the most tags removed (average corrections \pm SE; -0.02 ± 0.02 and -0.08 ± 0.09 , respectively) per image.

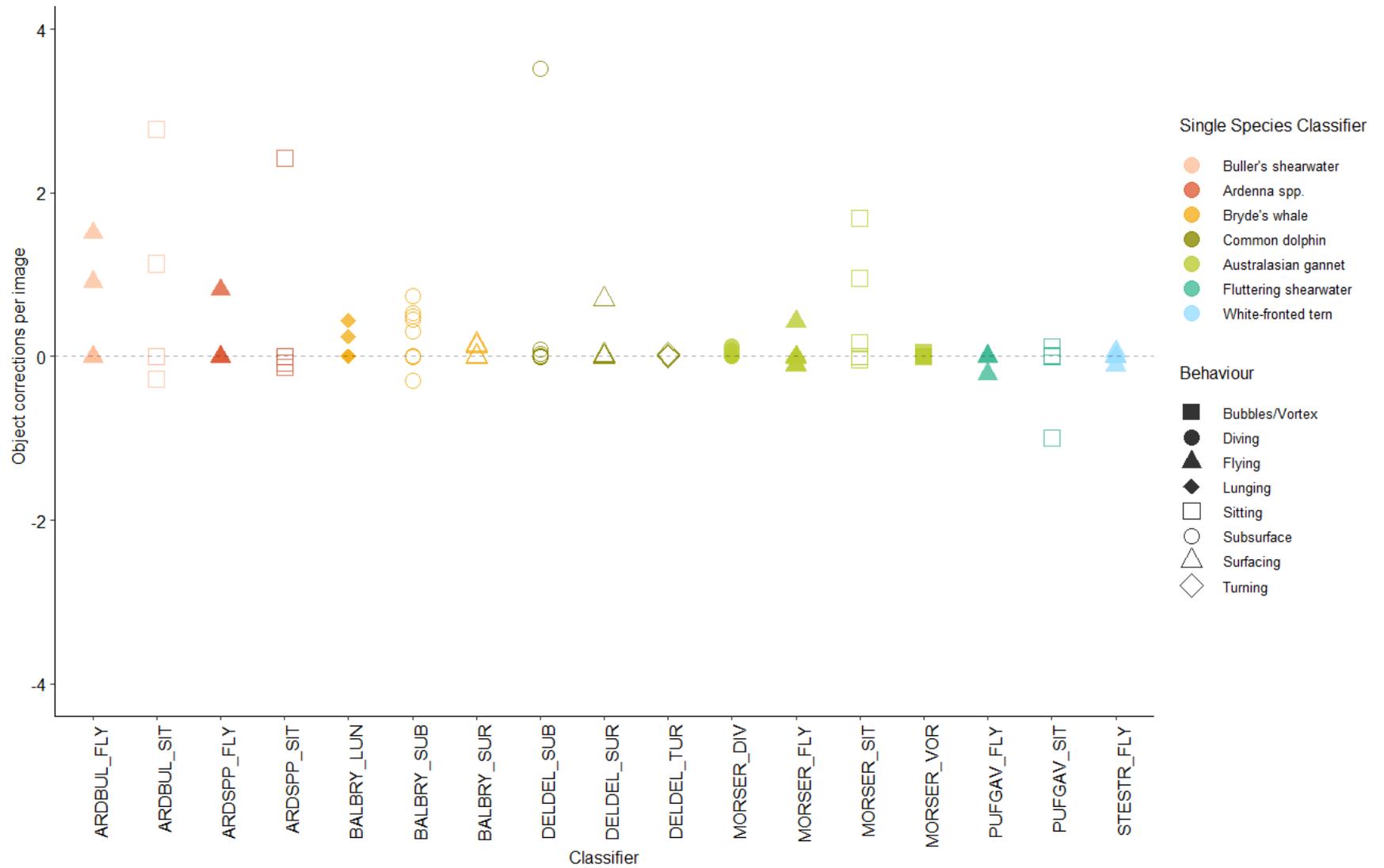


Figure 4.7 Directionality dot plot of the number of corrected annotations per frame, for each video clip auto tagged. The common name for each species is in the key and the classifier is on the x-axis.

4.3.2 YoloV4 Model Results

As is the intention when using ML tools, the preliminary YoloV4 model (Appendix 4) shows increased model accuracy (mAP) with increasing objects tagged (Figure 4.8, Table 4.5).

Table 4.5 Objects and mean Average Precision (mAP) for YoloV4 and ResNet-50 models for different species and behaviour classifiers

Species name	Single species classifier	Behaviour	Classifier	YoloV4 - mAP 80.2%		ResNet-50	
				Images	mAP	Total images	mAP
Common dolphin	DELDEL	Subsurface	DELDEL_SUB	19863	91.38	23914	93.6
		Surfacing	DELDEL_SUR	3600	80.34		
		Turning	DELDEL_TUR	451	30.72		
Australasian gannet	MORSER	Flying	MORSER_FLY	10503	89.53	50084	98.4
		Sitting	MORSER_SIT	38143	97.08		
		Bubbles/Vortex	MORSER_VOR	1083	44.98		
		Diving	MORSER_DIV	355	44.44		
Fluttering shearwater	PUFGAV	Flying	PUFGAV_FLY	5661	73.51	12641	97.97
		Sitting	PUFGAV_SIT	6980	81.54		
Buller's shearwater	ARDBUL	Flying	ARDBUL_FLY	4618	93.19	10513	99.52
		Sitting	ARDBUL_SIT	5895	89.89		
White-fronted tern	STESTR	Flying	STESTR_FLY	7550	92.51	-	-
<i>Ardenna</i> spp.	ARDSPP	Flying	ARDSPP_FLY	3374	90.39	10895	99.63
		Sitting	ARDSPP_SIT	7521	92.63		
Bryde's whale	BALBRY	Subsurface	BALBRY_SUB	6821	92.33	8859	93
		Surfacing	BALBRY_SUR	1549	96.49		
		Lunging	BALBRY_LUN	489	82.69		

Model accuracy increased with the number of training objects; however, accuracy at different object counts varied by species and behaviour. The lowest accuracy classifier, dolphins turning (DELDEL_TUR), had well below the targeted 2000 images (n = 451) due to limited imagery available and had the lowest mAP of 30.72%. However, the lowest tagged objects were gannets diving (MORSER_DIV). This was due to the gannets only being in the 'diving' position for a few frames at a time, limiting the available imagery, thus limiting the mAP to 44.4%. Body morphology, size, and the number of pixels a species takes up influence the mAP. Bryde's whales had a low number of objects (n = 489) for lunging (BALBRY_LUN) yet had an accuracy of 82.69%. The highest mAP (97.1%) in this model was gannets sitting (MORSER_SIT), which was unsurprising as it had the highest number of objects (n = 38,143) trained.

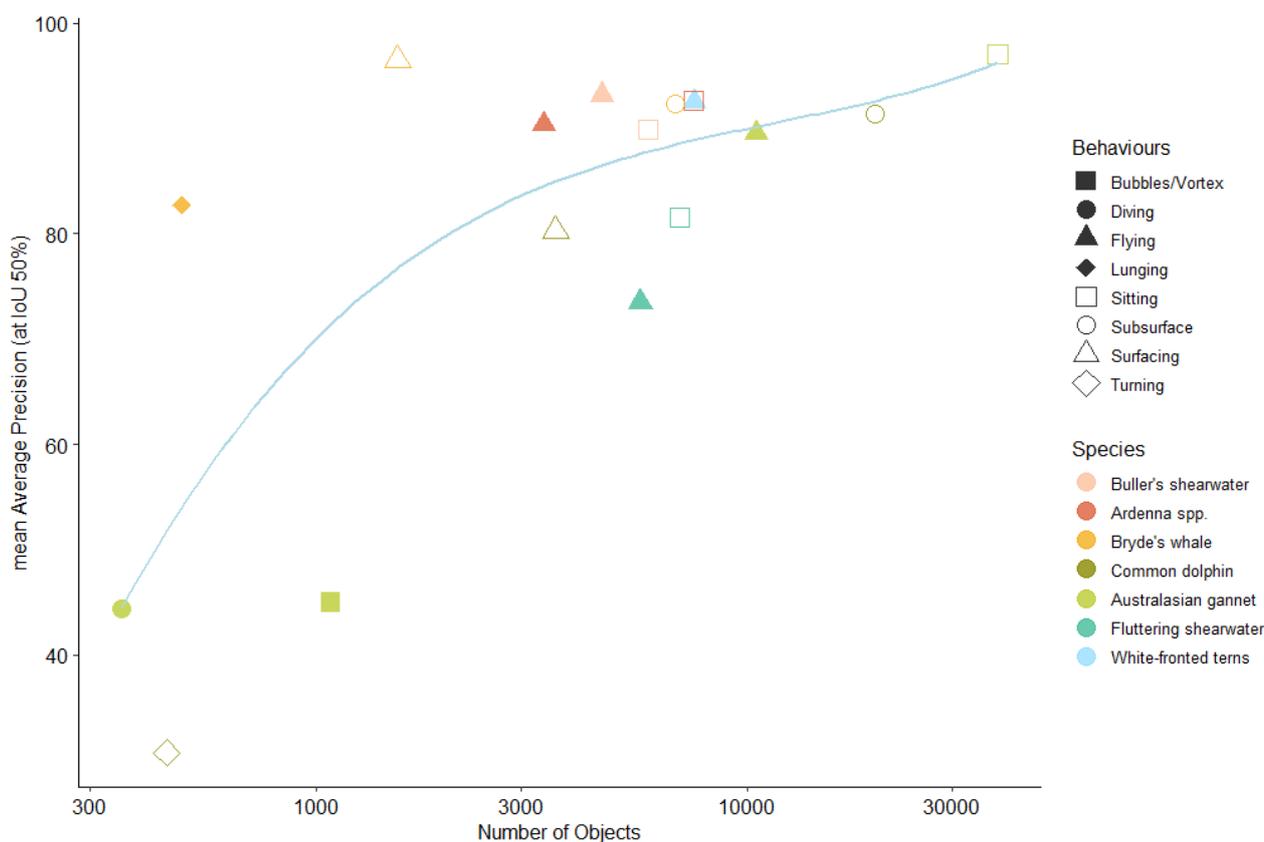


Figure 4.8 Accuracy (mAP) of the preliminary model (YoloV4) to detect behaviours of two cetacean and five seabird species with total number of objects used to train that classifier.

Using the YoloV4 model, we found that model accuracy was improved through resolution more so than adding additional layers. The limited precision of the model to detect some classifiers was improved upon with the addition of more objects, and the next steps of this study will be to continue to add objects to increase the accuracy of the model. As the number of iterations (batches) increases, as does the mean average precision of the model (red), with the measure of model error (loss) decreasing with each iteration. Our first YoloV4 CNN model had 53 layers and a resolution of 1280 x 1280 pixels. This model outputted an overall mAP of 41.3% and loss of 4.2008 after 40,000

iterations (Appendix 2). The model was then adjusted by increasing the resolution and reducing the number of layers – with the resultant model having 29 layers and imagery at a resolution of 816 x 816 pixels. The model accuracy improved to an overall mAP of 46.7% and loss of 0.9474 after 40,000 iterations (Appendix 3). When doubling the resolution to 2016 x 1152 pixels, the model accuracy increased to an overall mAP of 80.2% and an average loss of 0.7785 (Appendix 4). This high-resolution model formed the final YoloV4 CNN used in this study. By further increasing the dataset (iterations) to 60,000 images, the model was further increased in accuracy to mAP 81.8% and 0.9838 loss (

Figure 4.8).

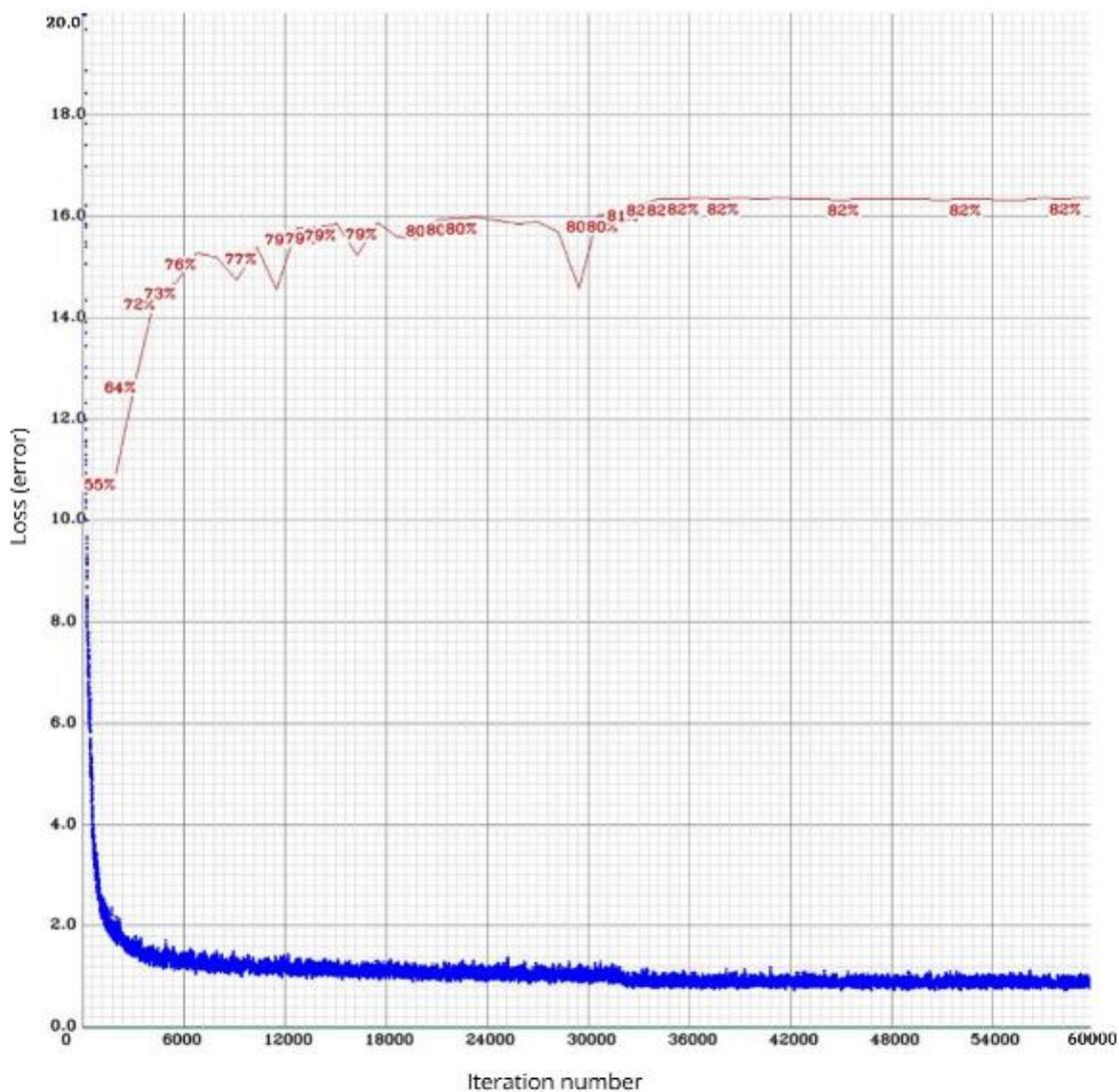


Figure 4.7 Accuracy (red) and loss (prediction error, blue) of final CNN YoloV4 29-layer model classifier at 2016 x 1152 pixels.

4.3.3 ResNet-50 Model results

When developing the second stage classifier model, we combined all the existing objects, instead separating them by species rather than species and behaviour. This allowed us to have a larger data pool per single species classifier, with all species except Bryde's whales ($n = 8859$) reaching the 10,000-object goal (Table 4.5). The ResNet-50 model was run at a reduced resolution of 224 x 224 pixels and 50 layers of neural networks (Figure 4.8). By combining the species objects, we increased the mAP by species to 93% and above, for all species (Table 4.5). For this model (Figure 4.7), as the number of epochs increases, we see the model accuracy increase and loss (errors) decrease, highlighting the need for models to be run repetitively to increase the model's accuracy. The number of epochs required is dependent on the complexity of the data set; due to the complexities associated with marine imagery (i.e., variability in the background, body positioning, and changing oceanographic conditions), a greater number of epochs were required to have good accuracy. There is a clear difference between subsurface- and surface-dwelling species (Figure 4.9). Bryde's whales and common dolphins had higher errors and lower accuracy than seabirds (Buller's and fluttering shearwaters, *Ardenna spp.* and Australasian gannets) throughout the epochs. This is likely attributed to contrast and distinguishability being affected by surface conditions, water clarity and animal depth.

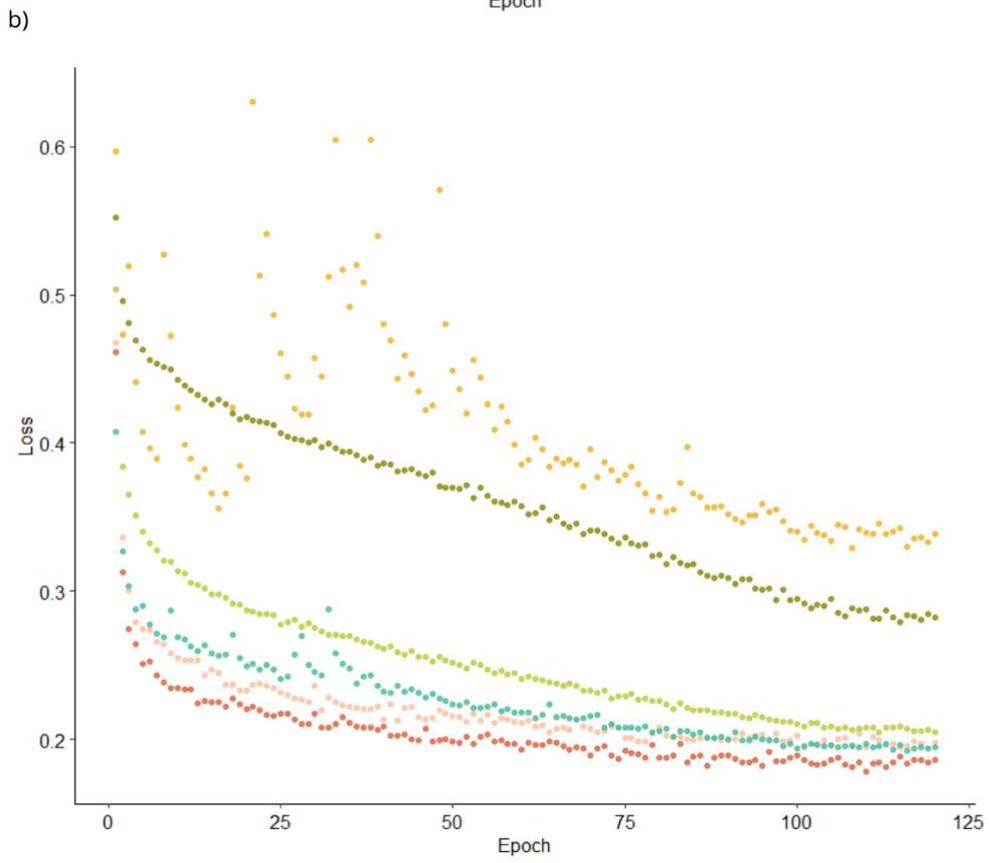
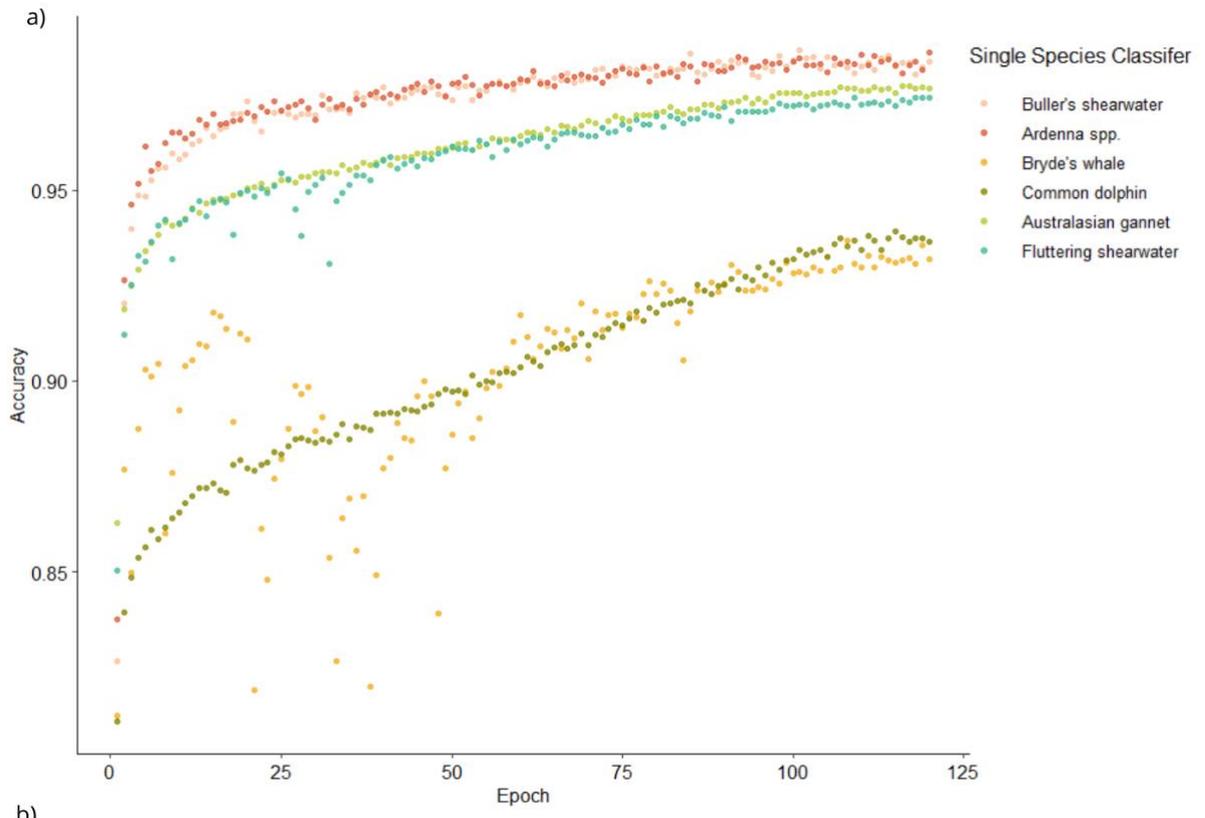


Figure 4.9 a) Accuracy and b) loss (prediction error) of ResNet-50 single species classifier model across training epochs.

4.4 Discussion

While Chapters 2 and 3 have focused heavily on the species and behaviours observed during MSFA events, we wanted to investigate new ways to survey, monitor, and analyse observations within these events and beyond. Here, we have presented a tool for automating the analysis of video frames with the final goal of detecting individuals and their behaviours for various taxa. Whilst drone footage was collected of MSFA events, we also recorded travelling, sitting, and milling behaviours, shifting the focus away from interpreting foraging events. Instead, we focus on the ability of AI tools to detect species and behaviours from drone footage. The results of this proof-of-concept tool are promising. From a minimum of 2,000 annotations per classifier, i.e., a particular species engaged in a specific behaviour, we successfully trained the AI tool to detect 11 seabird and six cetacean classifiers to varying degrees of accuracy. By further developing this model, we were able to achieve accuracies of >93% for all single species classifiers (five seabird and two cetacean classifiers).

Model design

Using the YoloV4 model, we found that model accuracy improved through resolution more so than adding additional layers. The mAP almost doubled, when increasing resolution of the images as the model has a greater ability to detect objects that may be cryptic or difficult to distinguish. Higher resolution images had the best performance in the YoloV4 model because it increased the distinguishability and detectability of features within images. The increased resolution was useful as there are morphological similarities between species e.g., white gannets and terns, and brown Buller's, fluttering, sooty and flesh-footed shearwaters. Likewise, for subsurface animals increasing image resolution was particularly important when the water and surface conditions impacted the clarity and contrast of the animal. The limited precision of the model to detect some classifiers will be improved upon with the addition of more objects in the next phase of this project.

Usability of AI in marine ecology

The drone and AI methodology proved effective for the post-analysis, detection, and identification of seabirds and cetaceans from aerial footage. CNN tools are useful for detecting frequently encountered species of which sufficient footage, and thus training and testing data sets can be obtained (Winkler & Vogelsang, 2016). For those with sufficient data, data augmentation was successfully applied to artificially increase the sample pool and variation in inputted footage (Krizhevsky *et al.*, 2012). Species in larger groups had a higher likelihood of being captured within the drone footage because the field of view at 30 m altitude was sometimes only able to capture a sub-sample of the MSFA. Those species and behaviours encountered more frequently were thus easier to collect sufficient footage, thus leading to a larger sample of video clips for CNN training and testing. As seabirds and cetaceans spend more time near the surface, increased contrast, clarity, and distinctiveness increases the likelihood of detection via drone (Corcoran *et al.*, 2021). Likewise, near-surface and nekton dwellers, such as sharks and rays, may spend time near the surface,

enabling them to be captured in drone imagery (Frixione *et al.*, 2020; Hawkes *et al.*, 2020). However, they were not present during our surveys and thus were not trained as classifiers in this study, although recent drone work on manta rays in the Gulf will be included as this AI project develops. This AI tool could be developed to accurately determine inter- and intra-specific interactions between multi-species assemblages of marine animals, which are by nature challenging to survey due to the high number of individuals and diversity of species (see Chapters 2 and 3; Camphuysen & Webb, 1999; Camphuysen & Garthe, 2004; Hamilton, 2020).

4.4.1 Precision of species annotations

Common dolphins and Bryde's whales spend time near the surface to breathe (Burgess, 2006; Izadi *et al.*, 2018; 2022), making it easier to collect sufficient footage to train the model. In our YoloV4 model, the accuracy for common dolphins ranged from 30.72% to 91.38%, with accuracy increasing with more images. The lowest classifier accuracy for dolphins was due to this classifier having fewer training objects than the 2000 object goal. For Bryde's whales, detection accuracy ranged from 82.69% to 96.49%, despite fewer trained objects overall. This difference is likely attributed to body size. Bryde's whales (~15 m) are significantly larger than dolphins (~2 m), thus taking up more pixels in individual frames and having higher resolution. The changes in body position of Bryde's whales during feeding, such as arched body, open mouth and extended throat pouch, are highly distinguishable from Bryde's whales which are travelling in a straight line, thus increasing the CNN's ability to distinguish between the different classes. Dolphins just below or at the surface foraging, turning, or surfacing have less obvious body changes and are therefore less distinguishable.

During early epochs, the CNN detected cetaceans with less accuracy and higher loss in comparison to seabirds. This was attributed to their sub-surface nature, with the animals' depth reducing the clarity and contrast of imagery. However, with increased model training, the accuracy improved to over 90%, highlighting the value of having image archives with sufficient variability and resolution of imagery, as seen in previous CNN research (Gray *et al.*, 2019a). Despite water depth, turbidity and surface conditions affecting our ability to see these animals when below the surface, their distinctive shapes and dark contrast to surrounding objects and backgrounds allowed the AI to classify them with high accuracy (>90%), (Barreto *et al.*, 2021; Corcoran *et al.*, 2021; Kelaher *et al.*, 2019). As camera resolution and imagery quality improve, the ability to post-process and detect species below the surface will also enhance, potentially revolutionising marine ecology and behavioural ecology studies (Joyce *et al.*, 2018; Oleksyn *et al.*, 2021).

Seabirds spend most of their time at or above the sea surface, with feather colouration, behavioural phenotypes and body size aiding in species identification and AI classification (Chabot & Francis, 2016). While drone-assisted monitoring for seabirds has been used extensively for nest surveys at seabird colonies (Brisson-Curadeau *et al.*, 2017; Parker & Huber, 2021; Weimerskirch *et al.*, 2018),

more work is needed to identify species and characterise behaviours during flights (Giacomo *et al.*, 2021). Precision was highest for those species with highly contrasting colouration and distinct patterns. For example, Buller's shearwaters were easily distinguishable when flying due to the distinctive dark 'M' pattern on upper wings; however, while sitting, they were visually similar to other sitting brown birds (Heather & Robertson, 2005; Marchant & Higgins, 1990). Species identification was aided by tracking the animal's movement across frames, particularly transitions between flying (wings outstretched – 'M' visible) and context-dependent size differences when sitting amongst heterospecifics. Those similar in colour, such as fluttering, sooty and flesh-footed shearwaters, are distinguishable by their small and large size, respectively, compared to other species in the frame (Marchant & Higgins, 1990). When no other comparable species are present, the altitude from which the footage was taken and behaviours should be considered, with higher altitudes changing the number of pixels an animal takes up in a given frame (Dujon & Schofield, 2019).

White-fronted terns and Australasian gannets both appeared as white teardrop-shaped birds when sitting; however, when flying, gannets have distinct black markings on their wingtips, and white-fronted terns have a forked tail. These morphological differences need to be considered by annotators when tagging each frame to ensure species are correctly classified when training the AI (August *et al.*, 2020; O. Hansen *et al.*, 2020; Ibraheem *et al.*, 2021; Schütz *et al.*, 2021). In our study, sooty and flesh-footed shearwaters were grouped due to their similar body size and colouration irrespective of behavioural state. With increasing camera quality, future studies and AI models may distinguish these species by their beak and feet colours (Marchant & Higgins, 1990). Fine-scale colouration and pattern differences may be used to determine species; however, flight protocols and image collection should be targeted to collect sufficient quality data for detecting those differences (Dujon & Schofield, 2019).

Common dolphins and Bryde's whales are found discontinuously throughout warm-temperate waters in New Zealand and around the world (Constantine *et al.*, 2018; Perrin, 2018), making our drone imagery of value beyond the Gulf. Similarly with the seabirds, Australasian gannets are morphologically similar to northern and Cape gannets, potentially highlighting the usability of this model for Australasian, South African (*M. capensis*), European and North American (*Morus bassanus*) populations of gannets. Sooty, flesh-footed and Buller's shearwaters are trans-equatorial migrants flying to the northern hemisphere during their non-breeding season (Gaskin & Rayner, 2013; Marchant & Higgins, 1990). Thus, the model can help detect these seabirds in their wintering grounds. Most fluttering shearwaters and white-fronted terns remain in New Zealand year-round; however, some overwinter in south-eastern Australia and eastern Tasmania (Berg *et al.*, 2019; Higgins & Davies, 1996; Marchant & Higgins, 1990). Thus, all the trained classifiers are applicable outside the study area, highlighting CNNs applicability to marine ecology studies beyond this thesis and beyond New Zealand.

4.4.2 Interpretation of behaviours from imagery

Behavioural ecologists seek to understand how animals behave, move, and interact in different environments with different sensory systems across time scales. The use of AI to detect animal behaviours offers an efficient approach to overcoming challenges in studying animal behaviour, particularly in marine environments (Dujon & Schofield, 2019; Oleksyn *et al.*, 2021; Schofield *et al.*, 2017; Vaughan *et al.*, 2022). As species exhibit different behaviours, we could not simply define the behaviours as 'active foraging', 'active non-foraging' and 'non-active non-foraging' like we did in Chapter 3. Instead, we chose to classify behaviours based on their body position in standalone frames (i.e., for seabirds: wings outstretched - flying, wings tucked in - sitting). We found that contextual effects of backgrounds, prey availability and intra- and inter-species interactions influenced our ability to distinguish species and their behaviours, even though we had broad descriptors as our classifiers (Colefax *et al.*, 2018). Environmental factors, such as surface glare and turbidity, differ between surveys and camera angles, and may affect wildlife detection and identification (Butcher *et al.*, 2019; Colefax *et al.*, 2018, 2019; Odzer *et al.*, 2022). For example, white-fronted terns and gannets were identified as false-positives in clips with surface glare, with white patches of sun glare resembling the shape of these white birds sitting. Likewise, surface waves and ripples were incorrectly classified for Bryde's whales below the surface, highlighting the importance of quality controlling the imagery used and error checking AI audited data, which is consistent with best practice for manually assigned classifications.

However, variation in classification precision was attributed to the distinguishability of behaviours and morphology of different species. Behavioural interpretations were limited by the number of pixels each animal consists of, which varied with the distance between the drone's camera and the animal (Nilsson *et al.*, 2015). Fluttering shearwaters were the smallest species trained in this CNN and were challenging to tag due to low contrast with the background and lack of distinctive shape and textural details (Stojnić *et al.*, 2021). Despite having >5,000 trained objects, flying and sitting classifiers had lower accuracy (73.51% and 81.54%, respectively) in comparison to other seabirds with similar numbers of manual tags. Animals that are large, bold and have greater contrast with the background of imagery are easier to detect and classify using AI tools (Chabot & Francis, 2016; Corcoran *et al.*, 2021). The dense flocking behaviours of gannets (Machovsky-Capuska *et al.*, 2014; Thiebault *et al.*, 2014) allowed us to collect sufficient footage to train sitting and flying classifiers to high precision (97.08% and 89.53%, respectively) but diving associated behaviours were less successful due to less available footage. The arrow-shaped 'diving' body position of gannets before water entry is difficult to capture as to control velocity, diving depth and angle they will only close their wings in the brief moments before diving (Machovsky-Capuska *et al.*, 2011a, 2013; Purvin, 2015). However, vortexing/bubble trails formed by cavitation (Batchelor & Batchelor, 2000) were quite persistent, lasting several seconds to minutes, indicating plunge-diving efforts (Machovsky-Capuska *et al.*, 2012). However, care must be taken when using trails as a proxy of animal behaviour as the bubble

trails outlast the duration the seabirds are beneath the surface (<13 seconds; Machovsky-Capuska, 2012). Behaviours that are not obvious to the naked eye proved challenging for AI classification. For example, some seabirds will often forage by plucking at the surface or dipping their head below the water (Camphuysen & Webb, 1999; Camphuysen & Garthe, 2004), creating a small splash that is difficult to distinguish from non-foraging splashes. Thus dipping (including plucking and seizing) was excluded for seabirds in this study.

4.4.3 Collecting footage

We found that ground sampling distance (Joyce *et al.*, 2018) affected image quality and detectability of small seabirds, with lower altitudes increasing the image resolution for capturing fine morphological differences and distinguishing species and behaviours. Future research should determine the altitude of UAV flights necessary to monitor the largest area possible whilst maintaining sufficient quality to identify fauna and their behaviours with AI tools (Barreto *et al.*, 2021). Increasing altitude made it more difficult to tag small seabirds, such as fluttering shearwaters, with the relative number of pixels and thus details decreasing with increased altitude. The resulting imagery was blurred when these birds were moving in the opposite direction to the drone flight path due to their rapid wing movements. Likewise, cryptic behaviours were difficult to detect with increasing altitudes, particularly the seabirds' dipping and surface plucking behaviours. For smaller animals, we recommend using higher quality cameras or flying at lower altitudes to improve object image quality and thus detectability of fine-scale features in the presence of variable environmental conditions and backgrounds (Petso *et al.*, 2021).

However, a balance between image acquisition and behavioural responses to the drone's presence must be achieved. The only response observed in this study was the occasional occurrence of black-backed gulls approaching the drone and vocalising for periods of only a few seconds, then flying away (pers. obs.). It is important to note that the dedicated observer never observed the approach distance to be of concern (Constantine, pers. comm.). It's well documented that cetaceans show little to no response to the presence of drones, even when the drone is flown at a low altitude (<10 m) (Castro *et al.*, 2021; Nowacek *et al.*, 2016). The value of drones for collecting data that enhances our understanding of cetacean behavioural ecology and demographics is well recognised (Gray *et al.*, 2019a; Johnston, 2019; Raudino *et al.*, 2019). Seabirds have different responses to the presence of drones with lower drone flight altitudes evoking stronger behavioural responses by some species (Giles *et al.*, 2021; Laborie *et al.*, 2021; Rümmler *et al.*, 2016). Responses are species and altitude specific (Rebolo-lfrán *et al.*, 2019), with responses varying from increased vigilance (Weimerskirch *et al.*, 2018), moving away from (McIntosh *et al.*, 2018; Pomeroy *et al.*, 2015) and attacking the drone (Marchowski, 2021). Generally, these responses to the drone are temporary, with the animals resuming pre-disturbance behaviour after removing the drone from the area (Marchowski, 2021; Weimerskirch *et al.*, 2018).

Drone survey plans need to consider target species' spatial and temporal movement ecology and the behaviours it aims to detect, particularly for elusive and low-density species (Baxter & Hamilton, 2018). Likewise, drone flights should collect representative reference footage with similar background conditions to which the AI model will be applied (Corcoran *et al.*, 2021). Dynamic and diverse reference footage allows the AI to detect objects of interest in various environmental conditions, object angles, orientations, and body positions (Gonzalez *et al.*, 2016). We found that ocean conditions such as whitecaps, surface glare, and turbidity, and highly active surface groups disrupted detectability, with splashes and bubbles increasing surface water disturbance (Joyce *et al.*, 2018). These issues can be overcome by collecting imagery across a range of contexts, of both active and non-active individuals, across non-linear background attributes (Salman *et al.*, 2020; Siddiqui *et al.*, 2018). Those who are seasonal migrants or have high site fidelity may be more challenging to get sufficient data for, and imagery may need to be controlled to target those species (Borowicz *et al.*, 2019; Cubaynes *et al.*, 2019).

4.4.4 Automated image tagging

Whilst the initial set-up of the CNNs is time-consuming and tedious at times, there are points during the pipeline of AI generation where the tagging process is sped up. The preliminary AI model was used to pre-tag images, creating bounding boxes and labels with associated classifiers, reducing the manual processing effort needed. Pre-tagging enabled us to visually inspect predicted bounding boxes, revealing insights into the reasons for false positives and negatives, including visually similar species or rarely sighted species with a low number of images available for training (Villon *et al.*, 2020). Upon inspection, we found that the model struggled to detect species against more heterogeneous backgrounds and in low contrast imagery, such as white gannets flying over patches of the ocean with high levels of glare, as seen in other studies (e.g., Butcher *et al.*, 2019; Colefax *et al.*, 2018; Hamel *et al.*, 2021). A minimum of ~2,000 annotations were tagged per classifier to balance the data, with augmentation increasing variability in the data set (Mikołajczyk & Grochowski, 2018; Shorten & Khoshgoftaar, 2019). The use of augmentation in CNN development reduces the manual tagging effort required to accurately train CNNs and overcome data deficiencies (Shorten & Khoshgoftaar, 2019).

4.4.5 Future steps

One of the many benefits of CNNs is their scalability. Creating open-source frameworks, combined with shared training datasets and thus trainable classifiers, will enhance our ability to detect animals and their behaviours from drone footage (Bravo Sanchez *et al.*, 2021). With greater data sharing, machine learning tools will be trainable across many species, behaviours, and environmental contexts, removing barriers associated with data collection for cryptic and low-frequency behaviours. Through collaboration, efficient and appropriate CNN models can be developed - driving further

advances in marine ecology and behavioural ecology studies (Valletta *et al.*, 2017; Weinstein, 2018; Johnston, 2019).

The model we present here can be further developed by adding new classifiers, and adding objects to existing classifiers, increasing their detectability in different oceanographic conditions and foraging contexts. As behavioural analysis and computational capacities improve, rapidly identifying species and their behaviours using these CNN tools can increase the amount of information extracted from imagery (Schmidhuber, 2015; Valletta *et al.*, 2017; Weinstein, 2018). Machine learning tools for detecting animals of interest are enabling reliable analysis of video footage from camera traps (Schneider *et al.*, 2018; Tabak *et al.*, 2019; Whytock *et al.*, 2021), time-lapse videos (Weinstein, 2018) and baited (Connolly *et al.*, 2021) and unbaited underwater cameras (Sheehan *et al.*, 2020). These AI tools can be further trained to detect three-dimensional action, using postural dynamics to classify observed behaviours (Berman *et al.*, 2014; Kim *et al.*, 2022; Stern *et al.*, 2015). Likewise, sequences of frames can be used to track animals and their postural movement, allowing AI and qualitative models to interpret the observed behaviours and accurately classify them (Matetić *et al.*, 2004). With the rapid growth and development of AI, we look forward to being able to use AI to audit drone imagery in the near future to better understand community dynamics and species behaviours.

4.4.6 Conclusions

Improvement and enhancement of images over time will play an important role in developing the ability of CNN tools to detect and identify different classifiers accurately. Here we show that CNNs are a viable methodology for detecting phenotypically diverse seabird and cetacean detections, from 40 cm fluttering shearwaters to 15m long Bryde's whales. The trained classifiers are useful for marine ecology studies beyond the Gulf as all the species trained in this model can be found outside the Gulf region. For the cetaceans, Bryde's whales (Constantine *et al.*, 2018; Gonçalves *et al.*, 2016) and common dolphins (Perrin, 2009) have a wide coastal distribution, inhabiting warm-temperate waters across the world's ocean. Incorporating AI-assisted aerial surveys can be a powerful tool to enhance future cetacean survey efforts across various habitat types.

Partnering machine learning and drone flights is potentially a very cheap, powerful, and accurate monitoring tool, reducing manual processing time and increasing the capacity of researchers to detect fine-scale behaviours and patterns of associations and community composition. Likewise, frame-by-frame visualisation of behaviours further enables annotators to see discrete behaviours and interactions, which may be challenging to observe in real-time. We anticipate that these higher-level features can be classified directly using the machine learning tools with further development. Likewise, the development of tracking and nearest neighbour analyses can open the door for analysing behavioural activity budgets and activity patterns (Fiori *et al.*, 2020; Torres *et al.*, 2018; Valletta *et al.*, 2017). With careful development and evaluation in different environmental contexts,

this state-of-the-art tool can fully automate the labelling of marine predators from drone imagery with human-like accuracy, revolutionising animal behaviour studies.

Chapter 5 General Discussion

5.1 Overview

In this thesis, we aimed to fill knowledge gaps for multi-species foraging associations (MSFA) in Tīkapa Moana – Te Moananui-ā-Toi, the Hauraki Gulf. The primary objective was to evaluate the composition and behavioural dynamics within MSFAs in the Gulf using a combination of boat-based focal follows, drone imagery and machine learning tools. By analysing MSFA dynamics from September 2019 to August 2021, there is compelling evidence that species' associations are based on prey type, abundance, and seasonal movement patterns. Variation in community networks provides insight into species interactions across ecological gradients, providing new insights into the effects of prey type and abundance, and seasonal movement patterns of species. Within communities, species play various roles, with the structure of assemblages shaped by positive and negative interactions (Bulleri *et al.*, 2016; Chilton & Sealy, 1987; Kneitel & Chase, 2004; Stachowicz, 2001). Through multitrophic approaches, the influence of prey on predators' association patterns can be better understood (Seibold *et al.*, 2018). MSFA association patterns in the Gulf were influenced by the available prey, with predators with similar prey preferences foraging together. Whilst the aggregation of species around a prey source is well-recognised in community ecology studies (Au & Pitman, 1986; Benoit-Bird & McManus, 2012; Clua & Grosvalet, 2001; Seibold *et al.*, 2018), studies of single species of large marine animals often dominate, as has been the case with most research in the Gulf until recently (Gostischa *et al.*, 2021).

The patterns of association and activity budgets we report here are based on the varied energetic requirements and morphological specialisations to capture prey at individual and population levels. Every individual has a role within an MSFA, such as a facilitator, disruptor, or scavenger, with many in these ephemeral communities relying on others to enable prey capture. For example, from our drone footage we see surface-feeding white-fronted terns (*Sterna striata*) waiting for fishes such as kahawai (*Arripis trutta*) to push their common larval fish prey to the surface, within accessible depths. Fluttering shearwaters (*Puffinus gavia*), however, sit on the surface, watching the terns as they fly above the kahawai; once the terns swoop down, the shearwaters use energy to efficiently fly over to forage, without needing to search for prey. Our focus on multiple species and their fine-scale patterns of association have not been described in such detail and provide a new way for people to think about the Gulf and its inhabitants. The combination of multidisciplinary tools will allow future investigation of MSFA drivers and dynamics, increasing accuracy and precision, allowing us to understand these associations better.

In Chapter 2, our boat-based focal observations revealed that foraging ecologies are essential factors that shape attendance patterns in marine predators, with eight distinct community types identified using the Bray-Curtis similarity index and SIMPER analysis. We found that species with similar foraging ecologies and dietary niches tend to forage together within MSFA events more often, having stronger social affinity indexes. Chapter 3 highlighted how these foraging ecologies shape activity budgets within MSFA events, with planktivores spending more time actively foraging than piscivores. The analysis of frequently attending species highlighted variation in activity budgets, with strong selective elements linked to prey type (Cairns, 1988; Fort *et al.*, 2011; Goodale *et al.*, 2019).

Chapter 4 shifted the focus to the feasibility of a novel, multidisciplinary method for analysing marine aggregations from a different angle to traditional boat-based observations using drone-based aerial imagery. The use of drones and machine learning tools should not be left unexplored as they are a powerful tool for marine ecologists and conservation biologists (Peters *et al.*, 2014; Tabak *et al.*, 2019). Although this work was a proof-of-concept chapter, many of the MSFAs presented in Chapters 2 and 3 have complimentary drone imagery, opening the opportunity for future comparative analysis. We found that machine learning tools are useful for analysing imagery collected from drones, reducing the large amounts of manual processing typically associated with interpreting large imagery datasets (Jordan & Mitchell, 2015; LeCun *et al.*, 2015). Together these three data chapters substantially advance our understanding of MSFAs in the highly productive but degraded Gulf, an internationally renowned hotspot for seabirds and cetaceans (Hauraki Gulf Forum, 2020).

5.2 MSFA dynamics

In past studies of New Zealand's MSFA events, analysis has focused on single species such as the Gulf's Australasian gannets (*Morus serrator*; Machovsky-Capuska, 2012; Purvin, 2015) and Bryde's whales (*Balaenoptera edeni brydei*; e.g., Izadi *et al.*, 2022; Wiseman, 2008), and dusky dolphins (*Lagenorhynchus obscurus*; Vaughn *et al.*, 2008). This study furthers our understanding of MSFA compositions by identifying seabird associations to a species level, enabling finer-scale studies to advance previous sampling protocols from a commercial whale watch tour boat where functionally similar taxa were grouped due to taxonomic resolution inconsistencies (Gostischa *et al.*, 2021). By focusing on more detailed data collection on MSFAs, we have expanded on the previous findings of three MSFA clusters to eight and captured fine-scale patterns of associations between species. We evaluated all species, focusing on frequent attenders (>5% MSFA events). We showed that Gulf MSFAs are dynamic at compositional and temporal levels, with described differences highlighting the influence of seasonal movements and prey specificity on MSFA dynamics. Rarely sighted species such as fur seals (*Arctocephalus forsteri*) and sharks were not detected within surveyed MSFA's, although aerial surveying is a better method for detecting patterns of shark residency and habitat use and drones will be valuable in the future (Hamilton, 2020; Stephenson *et al.*, In review). Although we had broad coverage of the Gulf, further MSFA research would benefit from the targeting of offshore,

pelagic and nearshore coastal MSFA events to gain a more complete picture of the whole region. Overall, the combination of different analytical approaches allowed us to expand the understanding of MSFA drivers and dynamics, using traditional species-specific analysis applied to entire communities.

Tools and analytical techniques

MSFAs are temporary and dynamic communities, with species attendance dependent on predator-prey and predator-predator interactions. We used the SOCPROG program to evaluate species co-occurrence patterns to better understand presence-absence associations between species (Whitehead, 2009). While this technique is typically used to assess conspecific association patterns (Brereton *et al.*, 2021; Degradi *et al.*, 2019), it proved helpful in visualising and evaluating species connectivity and association within MSFA events. Future research should incorporate Hidden-Markov Models to assess multi-scale patterns of occurrence and triggers of attendance and departure (Leos-Barajas *et al.*, 2017; Schliehe-Diecks *et al.*, 2012). Behavioural budgets using group-follows provide a unique insight into the benefits and trade-offs of foraging within MSFAs, with balances between interspecific associations reflected in the overall group behaviours (Cairns, 1988; Dunn *et al.*, 2020). We now know that within MSFAs, we can use the overall proportion of individuals performing a behavioural activity or state to gain an understanding of their foraging ecology and the trade-offs of MSFA participation (Chivers *et al.*, 2012; Collins *et al.*, 2016; Dunphy *et al.*, 2020). These behavioural budgets can be enhanced using technology-assisted focal-follows to follow individuals within large aggregations of marine predators. Drone imagery provides unique insights into animal association patterns and sub-surface behavioural dynamics, which are difficult to observe through boat-based observations (Butcher *et al.*, 2021; Colefax *et al.*, 2019; Torres *et al.*, 2018).

To better understand MSFA and social dynamics, techniques that facilitate individual focal follows in large multi-species aggregations are required. Commercially available lightweight drones are being increasingly used to monitor aspects of wildlife behaviour and demographics, providing novel insights into elusive and cryptic aspects of animal behaviour (Chabot & Bird, 2015). While there are concerns that drones cause behavioural disturbances, responses to drones are species and altitude specific (Castro *et al.*, 2021; Rebolo-Ifrán *et al.*, 2019; Weimerskirch *et al.*, 2018). When flown at species-appropriate altitudes, drone induced immediate behavioural responses can be minimised (Borrelle & Fletcher, 2017; Brisson-Curadeau *et al.*, 2017; Castro *et al.*, 2021; Krause *et al.*, 2021). Throughout our study, we saw no behavioural responses other than black-backed gulls (*Larus dominicanus*) occasionally displaying aggression towards the drone. Reflecting on this study, drones have an enormous potential for collecting data to support boat-based observations, capturing fine-scale, short-term behavioural interactions and providing insight into the role of sub-surface predators and schooling fish on MSFA dynamics.

Likewise, the use of telemetry in future research would enhance our understanding of movement patterns in the Gulf, as seen in recent seabird and cetacean studies (Constantine *et al.*, 2015; Dunphy *et al.*, 2020; Izadi *et al.*, 2018; Rayner *et al.*, 2015). Using animal-borne GPS loggers, behavioural and movement patterns can be inferred, with models and AI tools enhancing the ability of researchers to automatically detect and record targeted behaviours (Dunphy *et al.*, 2020; Korpela *et al.*, 2020; Shuert *et al.*, 2018; Vacqu  -Garcia *et al.*, 2015; Zhang *et al.*, 2019). Using telemetry, patterns of spatial associations within and between individuals can be inferred, enhancing our understanding of MSFAs, association dynamics, and potential threats (Mourier *et al.*, 2017; Robitaille *et al.*, 2018; Shizuka *et al.*, 2022).

Indicators of foraging conditions can be understood through stress hormones, with marine predator stress reflecting foraging conditions, cumulative stressors at lower trophic levels and environmental changes (Romero & Romero, 2002). Foraging conditions are reflected in baseline corticosterone levels which mediates fitness through the timing of reproduction and balancing parental and personal maintenance investment (Dunphy *et al.*, 2020; Immer *et al.*, 2021; Sorenson *et al.*, 2017; Storey *et al.*, 2017). Using stress hormones as ecosystem indicators, a comprehensive understanding of species- and context-specific foraging conditions can be obtained and used to inform conservation management plans (Hayden, 2021; Lukies, 2019; Madliger & Love, 2014; Whitehead *et al.*, 2022).

The use of these multidisciplinary tools and technology in future research will provide researchers with opportunities to better understand movement and foraging patterns in relation to ecosystem health, oceanographic and environmental constraints, and anthropogenic stressors (Hays *et al.*, 2016; Hussey *et al.*, 2015; Whoriskey *et al.*, 2022).

5.3 Environmental influences

Previous Gulf studies have found that zooplankton abundance and distribution is influenced by seasonal shifts in oceanographic conditions, with primary productivity having a bottom-up effect on the distribution of zooplankton and their predators (Carroll *et al.*, 2019; Chang *et al.*, 2003; Dwyer *et al.*, 2016; Stephenson *et al.*, in review; Zeldis & Willis, 2015). This study furthers those findings by looking at seasonal shifts within individual MSFAs and the likely triggers of any change. We found that communities vary by foraging ecology, with fish and zooplankton attracting piscivores and planktivorous species, respectively, and with generalists and scavengers foraging across both MSFA communities. Under warming ocean conditions and changing nutrient supplies, marine plankton distribution and richness are expected to shift, restructuring community composition with bottom-up effects on the functionality of marine food webs (Benedetti *et al.*, 2021; Cael *et al.*, 2021). Plankton community responses to degrading ocean conditions will be a critical component influencing future prey availability and association patterns. For example, the Bryde's whale and storm petrel association (Cluster a) identified in Chapter 2 reflects the shift in the predominant Bryde's whale prey

from fish to plankton over a ~ ten-year period, presumably in response to declines in fish prey availability (Carroll *et al.*, 2019; Gostischa *et al.*, 2021; MacDiarmid *et al.*, 2016). Seasonal variation in association and activity patterns was likely driven by a combination of energetic expenditure associated with breeding and offspring provisioning (Chivers *et al.*, 2012; Collins *et al.*, 2016), environmental conditions (van der Kolk *et al.*, 2020) and shifts in the distribution and availability of preferred prey (Colbert, 2019; Gulka *et al.*, 2020; Litzow & Piatt, 2003).

Many species are flexible foragers, altering foraging ranges to access more energy-rich and/or abundant prey. Under long-term changes in prey availability, gradual diet shifts have been observed in the Gulf's common dolphins (*Delphinus delphis*; Peters *et al.*, 2020) and Bryde's whales (Gostischa *et al.*, 2021). Short-term shifts in foraging behaviours allow species to cope with the increased energetic requirements of breeding, moulting and migrations. While increased foraging distance may incur extra costs, flexible foraging ranges and prey targeting can improve an individual's fitness when there are sufficient benefits. Foraging conditions are reflected in stress physiology, body condition and reproductive success, with changes in these measurements acting as indicators of ecosystem health. For example, targeting prey across different trophic levels or regions can improve body condition and reproductive success, as seen in the Gulf's common diving petrels (*Pelecanoides urinatrix*; Dunphy *et al.*, 2020).

In contrast, poor foraging conditions and nutritional stress is reflected in poor body condition and elevated stress hormones in grey-faced petrels (*Pterodroma gouldi*; Whitehead *et al.*, 2022) and little blue penguins (*Eudyptula minor*; Lukies, 2019). Incorporating these findings with dietary studies may provide insight into the energetic drivers of foraging within MSFAs and foraging and niche variation between specialist and generalist predators (Carroll *et al.*, 2019; Gostischa *et al.*, 2021; Terraube *et al.*, 2014). Stable-isotope analysis reveals changing diets and shifting trophic baselines over time, providing insights into marine predator trophic ecology and migratory behaviour (Newsome *et al.*, 2010; Newton, 2016; Rubenstein & Hobson, 2004). Incorporating stable isotopes to MSFA studies may reveal information about the foraging conditions of MSFA attendees, reflecting the changes in foraging conditions over time (Rayner *et al.*, 2021).

The Gulf is an ecologically diverse environment, with many habitat types supporting a range of species, and diverse multi-species assemblages (Gaskin & Rayner, 2013; Gostischa *et al.*, 2021; Hauraki-Gulf-Forum, 2020). In the Inner Gulf, we found large aggregations of planktivores and piscivores, with predators aggregating based on prey, often across multiple trophic levels. Given this, more attention should be given to the interconnected drivers of productivity and stressors that marine predators face, who act as indicators of ecosystem health (Carroll *et al.*, 2019; Dunphy *et al.*, 2020; Hazen *et al.*, 2019; Zantis *et al.*, 2022). Past Gulf management plans have not effectively addressed connections between predator communities and stressors that cross trophic boundaries and the land-

sea interface (Aguirre *et al.*, 2016; Towns *et al.*, 2019). However, significant developments in the Hauraki Gulf Forum's management plan and response strategy to the Sea Change – Tai Timu Tai Pari Marine Spatial Plan aim to strengthen the management of land-based impacts (Hauraki-Gulf-Forum, 2020).

The identification of MSFAs as important foraging events highlights the need for sustainable management of prey to ensure that MSFAs can persist under changing ocean conditions. Species have been associating and foraging within MSFAs before human arrival, with the role of these communities shifting over time as habitats and prey availability have been altered. Since humans arrived in the Gulf, extensive recreation and commercial fishing pressures and landscape development have disrupted ecosystem health and driven shifts in MSFA communities (MacDiarmid *et al.*, 2016; Pinkerton *et al.*, 2012). Anthropogenic disturbances, both on land (i.e., urban development, forestry, and agriculture) and at sea (i.e., dredging, and fishing), have degraded the Gulf, leading to the loss of habitats (Aguirre *et al.*, 2016; Hauraki-Gulf-Forum, 2020; Morrison, 2021). Cumulative stressors, such as increased sedimentation (Lukies *et al.*, 2021) and a loss of habitat formers (i.e., mussel beds and seagrass; Karatayev *et al.*, 2021; Morrison *et al.*, 2014), further impact the distribution, abundance and composition of prey, undoubtedly putting additional pressures on marine predators (Hauraki Gulf Forum, 2020; Pinkerton *et al.*, 2012). As such, populations of large marine predators have substantially declined with ecosystem degradation, further driving food-web changes (Aguirre *et al.*, 2016; Hauraki-Gulf-Forum, 2020; MacDiarmid *et al.*, 2016). Under these changing conditions, communities have evolved to take on different behavioural roles, with shifts in prey availability and oceanographic conditions disrupting observed foraging behaviours and community dynamics.

Currently, stock assessments have not been made for species of small schooling fishes on which many of these MSFAs are centred (i.e., pilchards and anchovies, Fisheries New Zealand, 2021). While our research has indicated what the new 'normal' Gulf looks like, we can expect these MSFA communities to shift with further ecosystem changes and climate-driven biodiversity shifts (Colbert, 2018; Lundquist *et al.*, 2011). The cumulative effects of nearshore degradation will further impact foraging behaviours within coastal MSFAs, highlighting the need to include efforts on nearshore species (Dwyer *et al.*, 2014; Hamilton, 2020; Lukies *et al.*, 2021; Wilson *et al.*, 2022). Likewise, feedback loops are evident on islands, where seabirds influence nearshore health, transporting nutrients between marine and terrestrial habitats through guano, promoting nearshore phytoplankton growth (Passuni *et al.*, 2021; Shatova *et al.*, 2017; Wing *et al.*, 2014). As island restoration and predator control efforts improve, increased seabird populations may contribute to increased health and prey availability in nearshore habitats (Bosman *et al.*, 1986; Gaskin, 2021; Hauraki-Gulf-Forum, 2020; Otero *et al.*, 2018).

Despite being designed to protect the Gulf, the Hauraki Gulf Marine Park has experienced radical changes, with recreational and commercial fishing allowed to continue, with only a handful of marine protected areas in place, which are too small to effectively protect large marine animals. There is no doubt that the Gulf is degraded, with marine predators, such as seabirds, cetaceans and elasmobranchs acting as indicators of the decline of the Gulf's health. It is too late to reverse the effects of many of these changes in the marine park. For example, ship strike mortality of the Gulf's Bryde's whales has been eliminated through voluntary ship speed reductions (Constantine *et al.*, 2015; Ebdon *et al.*, 2020). Likewise, mammalian pest eradication on islands has allowed native animals to recover, creating safe havens for breeding seabirds (Bassett *et al.*, 2016; Borrelle *et al.*, 2015; Gaskin, 2021).

The incorporation of new technologies and information systems can help prioritise conservation and restoration work, with up-to-date information helping researchers and managers prioritise decision making. Large marine animals are often widely distributed in open-ocean, remote, and difficult-to-access locations. Thus, aerial surveys, drones and AI technology can provide novel platforms to observe marine predators and advance our understanding of marine species and habitat health in the Gulf (Geoghegan *et al.*, 2018; Krause & Hinke, 2021; Stephenson *et al.*, in review; Ventura *et al.*, 2018). The use of drones and AI is already proving useful in monitoring the distribution and abundance of critically endangered Māui dolphins (*Cephalorhynchus hectori maui*; Constantine, pers. comm; <https://www.maui63.org>).

5.4 Limitations

Our observations of who is present may have missed cryptic species. However, we are confident the risk of missing or misidentifying species was reduced through having multiple observers (Kavanagh *et al.*, 2016). At any time we were unsure, such as when identifying sooty and flesh-footed shearwaters, and black petrels, we took photographs to detect distinguishing features. The lack of data collection during COVID 19 restrictions may have resulted in an underestimate or lack of recording of those species that occur seasonally in the Gulf. The seasonality of some species' attendance in a certain area should be considered when planning temporal aspects of future research. Continuing surveys will provide opportunities to capture rarer or less frequent attenders, including migrants and vagrants. Seasonal trends of MSFA compositions coincided with annual migrations of key species, including Buller's, flesh-footed and sooty shearwaters – further highlighting the need for future studies to consider the movements of these species. Localised movements of non-migrants should also be considered as seasonal trends in attendance may coincide with shifts in prey availability and distribution (Carroll *et al.*, 2019; Dunphy *et al.*, 2020; Heupel & Hueter, 2002). Schooling fish stocks are critical in maintaining biodiversity and ecosystem health, often forming the prey basis for MSFA events. Schooling fish act as valuable ecosystem indicators, reflecting stressors and bottom-up controls of higher-level predators and thus, their roles in MSFAs warrant further

investigation (Friesen *et al.*, 2017; Gaskin, 2017; Kozmian-Ledward *et al.*, 2020; Stephenson *et al.*, in review).

In this study, we covered extensive areas of the Gulf. However, research was largely focused on the inner Gulf. Across this area, oceanographic conditions and processes support a range of species and prey communities. Food-web dynamics and prey communities vary spatially throughout the Gulf based on nutrient flow and oceanic conditions, in particular, in the outer Gulf and entrance to the Firth of Thames, both of which were outside the surveyed area (Carroll *et al.*, 2019; Chang *et al.*, 2003; Zeldis & Swaney, 2018). The shifts in prey availability and oceanographic features influence community structures, with deeper water, pelagic predators and shallow water, coastal predators engaging in multi-species associations outside our surveyed range. For example, manta (*Manta birostris*) and spine tailed devil rays (*Mobula japonica*) are seasonally abundant in pelagic waters of the Gulf, foraging in association with planktivorous seabirds and Bryde's whales (Setyawan & Constantine pers. comm.; Duffy & Abbott, 2003). Likewise, despite the reported pelagic and offshore distribution of false killer whales (*Pseudorca crassidens*), they use the inner Gulf, foraging alongside offshore ecotypes of bottlenose dolphins (Zaeschar *et al.*, 2013, 2014). Expanding studies to offshore areas would also capture more data on pelagic and nocturnal foragers such as black (*Procellaria parkinsoni*) and grey-faced petrels (*Pterodroma gouldi*), which forage on the outer continental shelf break (Freeman *et al.*, 2010; Macleod *et al.*, 2008). Likewise, MSFAs involving nearshore, and highly coastal species, such as bottlenose dolphins (*Tursiops truncatus*; Berghan *et al.*, 2008; Dwyer *et al.*, 2014), little penguins (Lukies, 2019; McCutcheon *et al.*, 2011), and shags (*Phalacrocoracidae spp*; Lukies *et al.*, 2021; van der Reis & Jeffs, 2021), may have been missed due to survey routes tending to be further offshore. Future survey efforts should capture these nearshore communities to gain a complete picture of the diversity in MSFA dynamics. By combining technological advancements and new research and analysis approaches, we will be able to better understand future changes in MSFA community dynamics under different oceanographic conditions and levels of protection.

5.5 Next steps

Our study serves as a valuable database for detecting future changes in MSFA dynamics under changing ocean conditions. As improvements in ecosystem health are made, we will likely see these improvements reflected in MSFA dynamics. With greater awareness of marine issues and changing attitudes to marine conservation, we are seeing a greater push and action towards marine conservation and restoration in the Gulf. For example, benthic habitats, and thus seafloor biodiversity, are being restored through the addition of settlement substrate and cultured adult mussels (Sea *et al.*, 2022; Wilcox *et al.*, 2018); more marine protected areas are being developed to protect and restore fish stocks (Department of Conservation *et al.*, 2021); island habitats are being replanted and eradicated of pests (Bassett *et al.*, 2016; Towns & Ballantine, 1993); and communities are

implementing wide spread traditional management of declining kai moana species (Ministry for Primary Industries, 2021; Ngāti Manuhiri, 2022; Wilson *et al.*, 2007).

In the next steps of this work, we will be able to utilise the AI detection tool to investigate patterns of behaviours and associations within MSFA events. The accuracy of behavioural analyses would improve with the use of drones to conduct continuous focal animal follows and automated tools, such as AI (see Chapter 4), to audit patterns of activities within individual MSFA events (Hartman *et al.*, 2020; Ladds *et al.*, 2016; Wirsing *et al.*, 2022). By flying drones close to targeted species, we can observe and record cryptic species and behaviours which are, by nature, difficult to see when conducting boat-based observations (Butcher *et al.*, 2021; Corcoran *et al.*, 2021; Schofield *et al.*, 2017; Stephenson *et al.*, in review). Further AI model development will allow us to track and record the movements and behaviours of individual animals within a frame, automating the generation of activity budget and movement data (Bernardes *et al.*, 2021; Gabaldon *et al.*, 2022).

Machine learning is among one of many technologies which have the potential to revolutionise wildlife conservation, increasing the efficiency and scale of data collection and providing novel insights into environmental challenges, and translating data into meaningful action plans (Humphries *et al.*, 2018; Johnston, 2019; Speaker *et al.*, 2021; Tabak *et al.*, 2019). The generation of accessible ecological repositories of data and recognition and classification algorithms will further enhance the usability of AI, removing the need to completely start a model from scratch for each research project (Gray *et al.*, 2019a; Johnston, 2019; Valletta *et al.*, 2017; Weinstein, 2018). Further drone studies should ensure sufficient representative footage of targeted animals and their behavioural states are collected for object detecting machine learning tools to be trained.

The integration of multi-disciplinary techniques and perspectives, such as telemetry, stable-isotope analysis, behavioural data, stress physiology and Indigenous knowledge, will provide a more effective and holistic approach to determining the efficacy of conservation and management actions. This integration requires an open approach to sharing knowledge and maintaining long-term repositories of data. Making data available for the validation and reuse within and between disciplines can create opportunities for new collaborations, facilitating discovery, and furthering our perspectives on the same body of information, enabling us to use that information to maximise the impact and influence of the data to create meaningful change.

5.6 Conclusion

Ki uta, ki tai, from the mountains to the sea the Hauraki Gulf connects people through the abundance and diversity of life the oceans and land supports. The gulf has an extensive history of human settlement, from early Māori settling ~800 years ago to extensive coastal and urban sprawl and development in the current day. The extensive use and transformation of the Gulf is reflected in the

loss of shellfish beds, fish stocks and other marine life throughout the Gulf's waters (Hauraki Gulf Forum, 2020). Anecdotal evidence suggests that MSFAs have declined in size, duration, and abundance over time. It remains clear that better regulations and management are needed to enhance the future survival of marine biodiversity in the Gulf. However, hope is not lost, with changing attitudes towards marine conservation communities no longer accept this 'new normal'. Through the Revitalising the Gulf - Tai Timu Tai Pari Hauraki Gulf co-management plan, Indigenous approaches, and management strategies, such as marine protected areas, rāhui tāpu and mataitai, are being developed, and implemented, to protect and restore remaining habitats and species (Department of Conservation, 2021; Ministry for Primary Industries, 2021; Ngāti Manuhiri, 2022). With increased protection, the mauri of the gulf, its taonga, and the people it connects can be restored and preserved for future generations.

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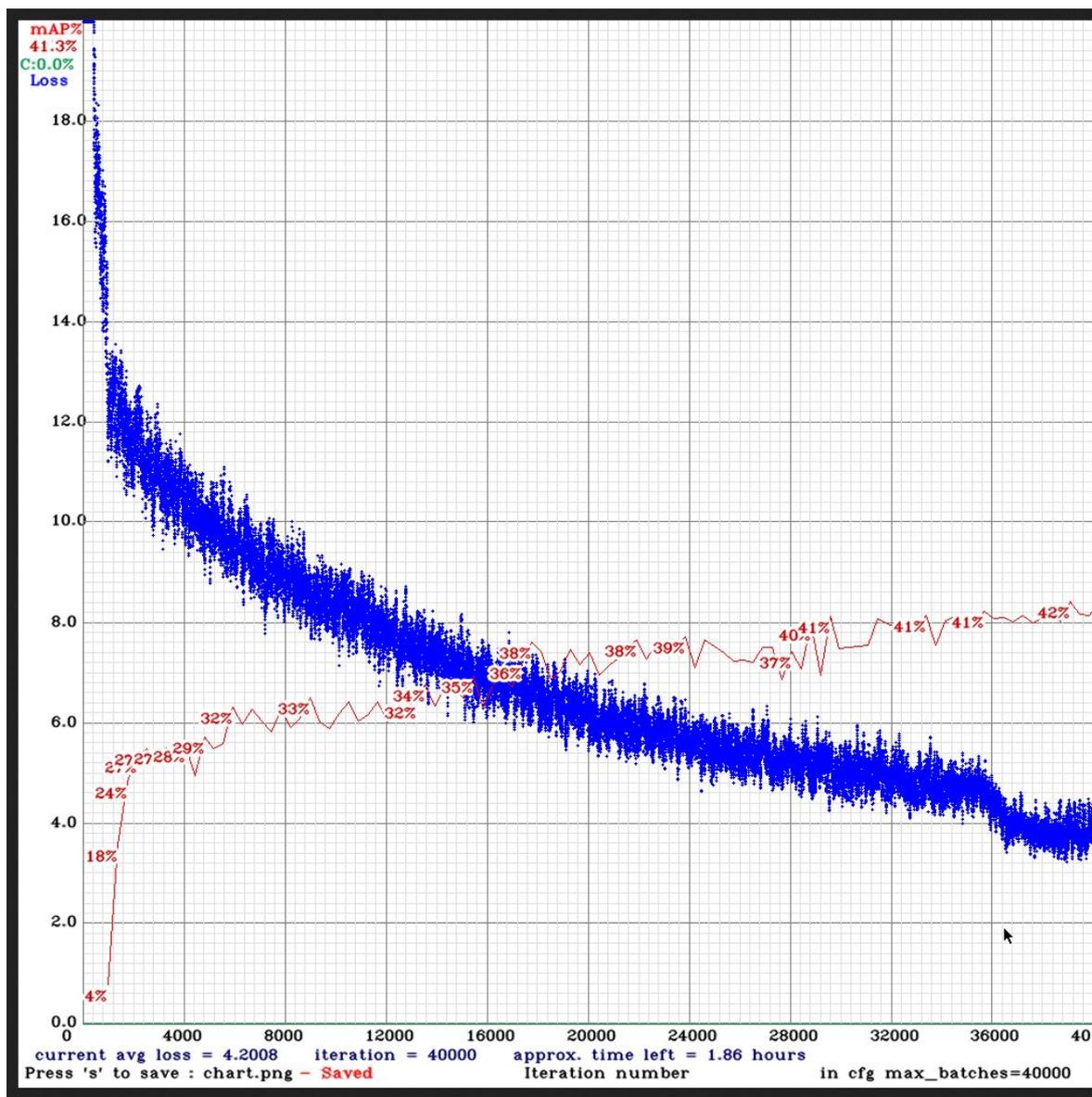
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Appendices

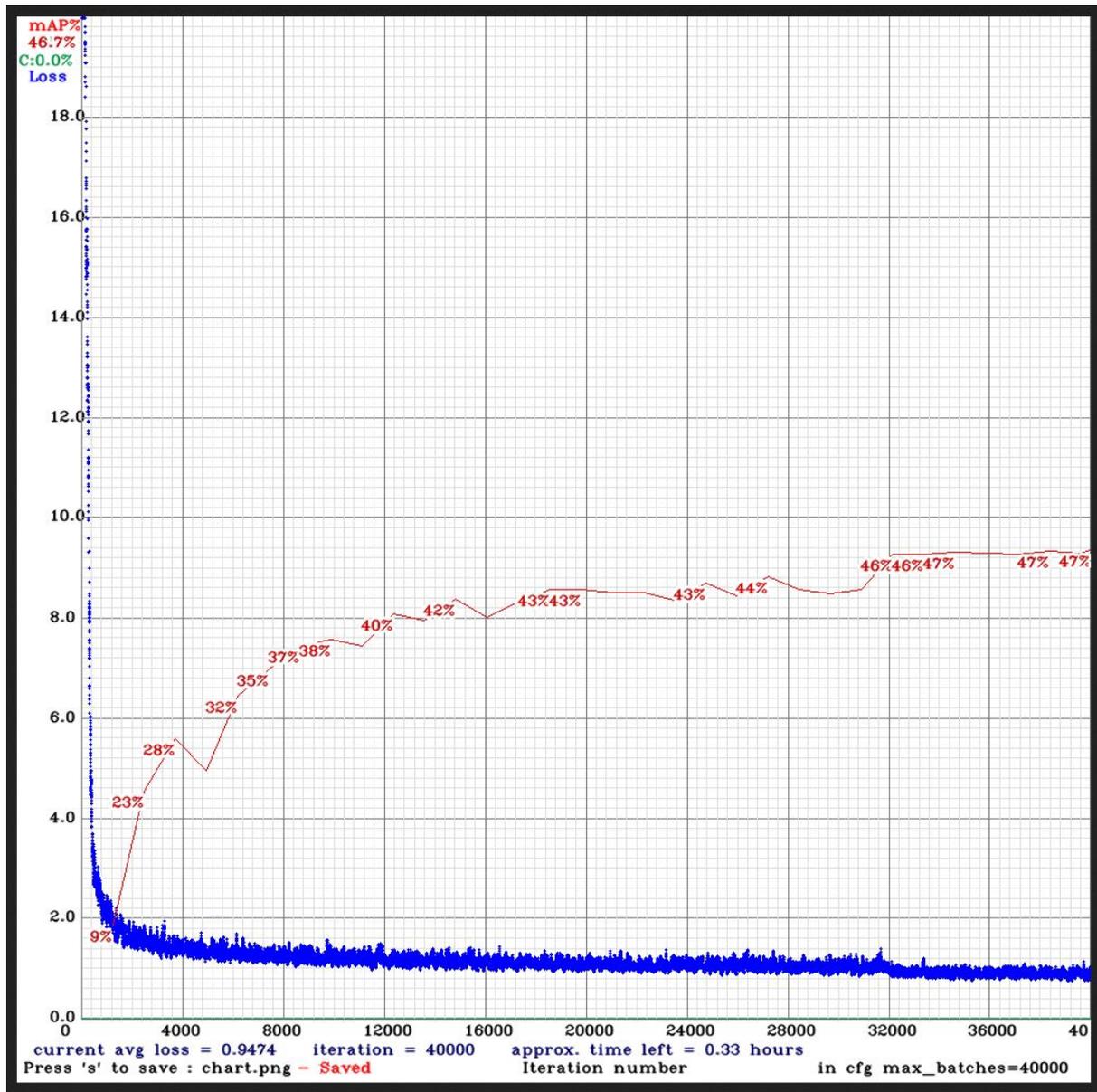
Appendix 1 Social affinity index between species (for species codes see Table 2.1; n = 22).

	ARDBUL	ARDCAR	ARDGRI	BALBRY	DELDEL	EUDMIN	LARDOM	LARNOV	MACHAL	MORSER	PACTUR	PELURI	PHAVAR	PROPAR	PTECOO	PTEGOU	PUFGAV	STESTR	STOPET	TURTRU	UNIDPE	
ARDCAR	0.61																					
ARDGRI	0.18	0.12																				
BALBRY	0.25	0.32	0.05																			
DELDEL	0.33	0.59	0.05	0.25																		
EUDMIN	0	0.11	0	0.05	0.14																	
LARDOM	0.22	0.24	0	0.16	0.47	0.04																
LARNOV	0.04	0.06	0	0.08	0.14	0	0.19															
MACHAL	0	0.04	0	0.05	0.03	0	0.09	0.07														
MORSER	0.46	0.59	0.1	0.36	0.9	0.13	0.46	0.18	0.03													
PACTUR	0.1	0	0	0	0	0	0	0	0	0												
PELURI	0.13	0.19	0	0.26	0.09	0	0.04	0	0.1	0.15	0											
PHAVAR	0.09	0.08	0	0	0.05	0	0.13	0.13	0	0.1	0	0										
PROPAR	0.05	0.04	0	0.06	0.06	0	0	0	0	0.05	0	0	0									
PTECOO	0.08	0.08	0	0.11	0.08	0	0.04	0	0	0.1	0	0	0	0								
PTEGOU	0.04	0.08	0	0.17	0.06	0	0.04	0.07	0	0.1	0	0.38	0	0	0							
PUFGAV	0.41	0.54	0.05	0.27	0.7	0.14	0.41	0.19	0.05	0.82	0.03	0.14	0.08	0.06	0.06	0.08						
STESTR	0.26	0.11	0.04	0.1	0.17	0	0.23	0.17	0	0.35	0	0	0.05	0.05	0	0	0.45					
STOPET	0.28	0.41	0	0.35	0.22	0.05	0.17	0	0.06	0.31	0.07	0.18	0	0.07	0.06	0	0.29	0.07				
TURTRU	0	0	0	0	0	0	0.04	0.17	0	0	0	0	0.14	0	0	0	0	0	0			
UNIDPE	0.05	0	0	0.06	0	0	0	0	0	0.03	0	0	0	0	0	0	0	0	0	0		
UNIDTE	0.08	0.11	0.11	0.11	0.11	0	0.04	0.13	0	0.15	0	0	0.09	0.14	0	0.11	0.14	0.04	0	0	0	0.17

Appendix 2 Preliminary model Accuracy-Loss graph (mAP: 41.3%; layers: 53; Pixels: 1280 x 1280)



Appendix 3 Preliminary model Accuracy-Loss Graph (mAP: 46.7%; Layers: 29; Pixels: 816 x 816).



Appendix 4 Preliminary model Accuracy-Loss Graph (mAP: 80.2%; Layers: 29; Pixels: 2016 x 1152).

