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INTRODUCTION

New Zealand dolphin *(Cephalorhynchus hectori)* is an endangered dolphin species. Like the other three *Cephalorhynchus* species, it is a very small dolphin - arguably the smallest dolphin in the world. All four *Cephalorhynchus* dolphins have small populations and a very small range, compared to other dolphin species. New Zealand dolphin is only found in New Zealand waters, *Cephalorhynchus eutropia* only in Chilean waters, and *Cephalorhynchus heavisidii* only off the coast of Namibia and South Africa. Almost all *Cephalorhynchus commersoni* are found in the waters of Argentina, with much smaller numbers in the Falkland and Kerguelen Islands. This limited species distribution places these dolphins at risk from human activities. Most other dolphin species have much larger distributions, with worldwide populations in the hundreds of thousands or millions of individuals. New Zealand dolphins number in the thousands (Dawson et al. 2004; Slooten et al. 2004, 2006), possibly as many as 15,000 individuals (MacKenzie and Clement 2014, 2016, 2019).

The North Island sub-species is called Māui dolphin. With a total population of 57 individuals one year and older (Cooke et al. 2019) it is Critically Endangered (Reeves et al. 2021). Several of the populations of the South Island sub-species Hector's dolphin are also very small and vulnerable. For example, there are an estimated 42 Hector's dolphins off Otago (Turek et al. 2013). Dolphin populations around the North and South Island of New Zealand are strongly fragmented, with a small number of relatively large populations, many small populations and some areas where the species appears to have been extirpated altogether (McGrath 2020). Small individual home ranges, on average 50 km of coastline (Rayment et al. 2009), lead to discrete local populations. Eight local populations of Hector's dolphins, right around the South Island, and one population off the North Island west coast have been studied using photographic identification. The results show that the same Hector's dolphin individuals are consistently seen year-round in the same geographical area (Bräger et al. 2002; Rayment et al. 2009; Bräger & Bräger 2018), with movements among local populations more than 100 km apart < 1% per year (Fletcher et al. 2002). This highly fragmented population structure is a risk factor in and of itself.

Hector's and Māui dolphins have been heavily impacted by mortality in fishing nets (e.g. Cooke et al. 2019; Slooten and Dawson 2010). Bycatch over the last four or five decades has resulted in dolphins declining to around 30% of original population size and Māui dolphins to below 5% of their former numbers (Slooten 2007, 2013, 2020; Slooten and Dawson 2010, 2020; Slooten and Davies 2011). The dolphins are caught in two different types of fishing nets: Gillnets and trawls. Gillnets are stationary in the water and made of very thin nylon mesh. The fish caught in these nets are too large for New Zealand dolphins to eat. Dolphins are caught when they accidentally venture too close to a gillnet. Trawling vessels drag large, heavy nets either along the seafloor or through mid-water. Dolphins are attracted to trawlers, which frequently have large groups of dolphins following the vessel, repeatedly diving down to the net. Occasionally they make a mistake and are caught in trawl nets.

Our analysis of the population effects of bycatch is based on knowledge of the spatial and temporal distribution of dolphins, gillnets and trawling vessels, and is validated using bycatch estimates from government observer programmes. The model landscape is shown in Figure 1. Bycatch data for the area to the north and south of Banks Peninsula (Figure 1) suggest that in recent years 37 Hector's dolphins have been caught in gillnet and trawl fisheries each year (TMP 2019). Survival rates have increased from 86% when there was no protection from fisheries bycatch to 91% with partial protection. This has reduced the population decline (Gormley et al. 2012), thus highlighting the need to prevent bycatch in certain areas. The model we present in this paper fills a gap in the tools that can be used for assessing whether conservation measures are sufficient to prevent future declines in different populations.

Populations of endangered species are typically small, making them vulnerable to demographic stochasticity. When individuals in these populations aggregate in areas that are exploited by humans, the need for careful spatially explicit conservation planning becomes critical. This can be achieved with agent-based models due to their ability to incorporate spatial structure (e.g. de Jager et al. 2019, Nabe-Nielsen et al. 2018, Railsback and Grimm 2019, van Beest et al. 2017). In most cases, the distribution of the species and the spatial pattern of human activity are critical to estimating the severity of the impact and the effectiveness of protection measures to reduce the level of impact. Therefore, an approach that explicitly maps the human activity and the species affected is needed.

Our main goal is to assess the effectiveness of protection measures introduced in 2020 that aim to reduce dolphin deaths in gillnet and trawl fisheries (Figure 2). These new regulations ban one or both of these fishing methods in part of the dolphins' habitat. We model a time period of 30 years to evaluate how population size changes over this period, in response to current dolphin protection as compared to protection measures proposed by the IWC (2018) and IUCN (2012). The patterns used as criteria for evaluating the model include population trends and the number of dolphins caught each year.

MATERIALS AND METHODS

Study species

New Zealand dolphin *(Cephalorhynchus hectori)* is found only in New Zealand waters. Data on their distribution and abundance are available from four series of population surveys (Dawson and Slooten 1988; Dawson et al. 2004; Slooten et al. 2004, 2006; Rayment et al. 2009; Turek et al. 2013; MacKenzie and Clement 2014, 2016, 2019). These surveys have produced detailed data on dolphin distribution, in relation to water depth and distance from shore, in areas with high dolphin densities. In low density areas, where aerial surveys have been much less effective, data from small boat surveys and acoustic detections confirm that dolphin distribution is similar with respect to water depth and distance from shore.There are a small number of relatively large populations, many small populations and some areas where the species was common in the past but very rarely seen today (McGrath 2020; Cooke et al. 2019; Turek et al. 2013; Threat Management Plan 2019). Offshore distribution data is available from the areas with highest dolphin abundance, the east and west coast of the South Island. In the shallower waters off the east coast, 41% of the population is found within 4 nmi offshore, 46% between 4 and 12 nmi offshore and 11% between 12 nmi and the 100m depth contour, with some 2% of the population in waters deeper than 100m. Off the west coast of the South Island, water depth increases more rapidly with distance from shore. Here 76% of the population is found within 4 nmi offshore, 22% between 4 and 12 nmi offshore and 2% between 12 nmi and the 100m depth contour, and no dolphins have been sighted in waters deeper than 100m.

Individual home ranges are on average only 50 km of coastline (Rayment et al. 2009). Males are slightly smaller than females, which helps to explain why mate monopolisation does not appear to be a feature of the reproductive behaviour of male Hector's dolphins (Slooten 1991). When male cetaceans have to search for sexually active females, rather than being able to defend them from other males, the fertilization rate of the population depends in part on the amount of time needed for a male to travel between groups, relative to the length of time each female is fertile and the degree of synchrony among females (e.g. Whitehead 1987, Whitehead and Weilgart 2000). Such a mating system is likely to result in an Allee Effect with relatively high fertilization rates in areas where Hector's dolphins are common and a lower fertilization rate in low-density areas (Slooten 1991). Local extirpations also suggest that Allee Effects influence the dynamics of very small Hector's and Māui dolphin populations.

Estimates of group size, movements, survival and reproductive rates are available from 35 years of monitoring Hector's dolphins (e.g. Slooten 1991, Slooten and Lad 1991, Gormley 2009). Data on the distance dolphins move per hour fits a Weibull distribution, with random hourly movements typically 1 km or less (de Jager et al. 2019). It is rare for all or most individuals in a Hector's or Māui dolphin group to be moving in the same direction and continue to do so for any length of time. Dolphins occasionally travel in one direction for half an hour or so, but their typical behaviour resembles a 'random walk' - moving in one direction and then back again. Females give birth to their first calf at age 7-9 years and have one calf every 2-4 years. In a sample of 9,036 Hector's dolphin groups observed in the wild (by the senior author), groups of up to 10 individuals were by far the most common (>60%) and groups of more than 50 individuals were rarely observed except when following trawlers (Figure 3).

Fisheries and bycatch

Bycatch estimates come from government observer programmes (e.g. Threat Management Plan 2019, Roberts et al. 2019, Starr and Langley 2000, Baird and Bradford 2000). The area north and south of Banks Peninsula (Figure 1) has received far more observer coverage than any other area. Observer coverage is typically low in inshore fisheries in New Zealand, on the order of 5% or lower for most areas and years. However, the Banks Peninsula area has had relatively high levels of observer coverage, with almost 40% coverage in 1997-1998. When a dolphin encounters a gillnet or trawling vessel, there is a small probability that the dolphin will be killed. The probability of capture is based on New Zealand government estimates of the number of dolphins caught in each of these fishing gears. The official government estimate of Hector's dolphin bycatch in this area is 37 per year (Threat Management Plan 2019) with 17 (5th to 95th percentile 8-33) caught around Banks Peninsula and 20 (8-42) to the south of the peninsula. Nationwide estimates of Hector's dolphin bycatch are 44 dolphins (21-80) caught in commercial gillnets and 14 (1-43) in trawl nets each year, with Māui dolphin bycatch estimated at 0.10 dolphins per year (0-0.25) in commercial gillnets and 0.02 (0-0.05) in trawl nets each year (Threat Management Plan 2019). The previous government estimate was 110-150 Hector's and Māui dolphins caught each year during 2000-2006 (Davies et al. 2008), with 35-46 of these caught on the east coast of the South Island (Slooten and Davies 2012).

Estimates of trawling and gillnetting effort in each area are available from the Ministry for Primary Industries (MPI 2020) and other official sources (Dragonfly 2020). Following a substantial change in dolphin protection in 2008, there have been on average 2,481 trawl events per year on the north side of Banks Peninsula and 5,081 events per year to the south of Banks Peninsula (i.e. 6.8 per day in the north and 13.9 per day in the south). Gillnets stay in place for 1-3 days on average and then redeploy to a new destination. Dolphins are attracted to trawlers, with much larger groups of dolphins observed following trawlers than group size in the absence of trawlers (Figure 3). Trawlers fish over a distance of 10-30 km (mean 16.7 km) before hauling the net to transfer the catch into the boat (Figure 4). Dolphins are frequently seen following trawlers. The spatial distribution of fishing effort from 2009-2017 is shown in Figures 5 and 6.

The model assumes that there is no bycatch in areas where trawlers and/or gillnets are prohibited (i.e. in protected grid cells). This is optimistic, because illegal fishing is known to occur. Dolphin protection areas, where the use of gillnets and/or trawling are banned, have changed over the years (Figure 2). The user selects the starting year of the model, which determines initial dolphin protection. Protected areas were changed in 1988, 2003, 2008, 2013 and 2020 by Ministerial decisions to improve protection in those years. There was no dolphin protection before 1988.

Model description

We developed an agent-based simulation model to study how population growth rates for the New Zealand dolphin were influenced by different levels of protection from bycatch in gillnets and trawls. The model uses a spatial structure that matches data on the distribution of dolphins and fisheries, and builds on the processes that influence population dynamics in nature. In the following section we present a description of the model following the ODD protocol (Grimm et al., 2020). The model was developed using NetLogo (Wilensky 1999).

Purpose and patterns

The purpose of the model is to predict the impact of fishing on New Zealand dolphin populations under different levels of fishing. Dolphins are caught in two different types of fishing nets: Stationary gillnets and mobile trawls. Dolphins are attracted to trawl nets. The ultimate goal of the model is to provide a tool to prevent fisheries from having negative impacts on dolphin populations.

The model produces several patterns that emerge from the dolphins' movement behaviour: The dolphins' movements with regard to water depth and distance from shore drive their spatial distribution, replicating dolphin distribution data from surveys; their tendency to move towards trawlers influences the number of encounters they have with trawl nets, and therefore the risk of dying by drowning in a net. Second-tier patterns include the effect of dolphin distribution on their reproductive rate, with females breeding only if there is a male nearby. This results in very small populations going extinct if they are isolated from other dolphin populations.

Entities, state variables and scales

The following entities are included in the model: dolphins, trawlers, gillnets and grid cells. A grid of 1025 by 1025 grid cells represents the 1670 km^2 landscape of New Zealand waters (Figure 1). Each grid cell (1.63 x 1.63 kilometres) is characterized by the following state variables: Location, depth, distance to shore and protection status (ban on gillnets, ban on gillnets and trawling, or no protection). Just over 13% of the grid cells represent land.

Dolphin agents are characterized by their location, movement direction, age, sex, time to next giving birth to a calf (if female) and subspecies. There are two subspecies of dolphins in the model, Māui dolphins around the North Island and Hector's dolphins around the South Island of New Zealand. Each Māui dolphin agent represents one individual dolphin, whereas one Hector's dolphin agent represents a group of dolphins. Group size is determined by the distribution of observed group sizes from 9,345 encounters with Hector's and Māui dolphins between 1991 and 2020 (Figure 3). It is assumed that half of the dolphins are female. Trawler agents are characterized by their location and movement direction. Gillnets are characterized by their location and by the time until they redeploy to another location.

Process overview and scheduling

Each day, dolphins move and age (becoming one day older). Dolphins move an average of 2.5 km per day (Figure 4) drawn from a log-normal distribution, following random walks biased towards a home grid cell along the shoreline.

Dolphins have a probability to die of natural causes each day, with young and old dolphins more vulnerable. Once a female reaches maturity (7 years old), there is an annual probability of 0.25 - 0.50 that she will reproduce (equivalent to a 2-4 year calving interval, see Slooten et al. 2000). The day on which a female gives birth is drawn from a normal distribution with a mean of 45 and a SD of 2 days, where day 1 is 1 November and 120 is 28 February. This corresponds to an observed peak of breeding in December, with most calves born during November - February. For Māui dolphins a new individual agent is created, and for Hector's dolphin groups one individual is added to the list of dolphins represented by that agent. When a calf is born into a Hector's dolphin group, there is a probability that the group splits into two groups. The new group's size is drawn from a distribution representing group sizes observed in the wild, and this number of individuals is removed from the pre-existing group. Survival and reproduction are applied to individual dolphins, adding demographic stochasticity to the model. The probability that a female becomes pregnant is set to zero if the distance to the nearest male exceeds 50 km (the average home range).

After dolphins have moved, trawlers move following a random walk biased towards a home port. The distance covered by each trawler is drawn from a log-normal distribution, based on trawling data provided by MPI (Figure 4). Dolphins in grid cells directly on a trawler's path have a chance of being caught in the trawl net, as do dolphins within 2 grid cells either side of the path of the trawler. This represents the fact that dolphins are attracted to trawling vessels. Trawlers cannot travel onto land or protected grid cells, and instead continue the remainder of their movement by choosing a new heading (again, biased by distance from home port) that won't take them onto protected grid cells where trawlers are banned. Finally, gillnets act. Gillnets remain stationary for a variable number of days (with a peak of 1 day and a maximum of 3 days) and then reposition to a non-protected ocean grid cell within their fishing area. Dolphins on the same grid cell as a gillnet have a chance to be caught.

Model calibration and sensitivity analyses

The strength of the dolphins' attraction to their home patch (where they were initially placed on the map) is calibrated within the model to ensure the average dolphin home range matches the observed average home range (50 km) and dolphin distribution matches the population survey data. As a result, the model replicates dolphin distribution in well studied areas, by tuning the behaviour at a level of complexity lower than the observed pattern and then generalising to areas with less data on spatial distribution. The probability of dolphin attraction to trawlers is calibrated within the model to match field observations of groups of dolphins feeding close to trawl nets (Figure 7). The probability of a dolphin dying when it is in the same location as a trawler or gillnet was estimated in the Banks Peninsula area (Yellow box in Figure 1). This is the only area with sufficient observer data to result in scientifically robust estimates of dolphin deaths in these two fishing gears. We estimate the capture probability for gillnets and trawlers within the model. That results in a total of 37 dolphins caught per year in this area, which is the official government estimate. We use this information to estimate the probability of capture when a dolphin or group of dolphins encounters a gillnet or trawler.

We carry out sensitivity testing to estimate the effectiveness of current protection given government estimates of bycatch, as well as bycatch levels more consistent with recent reports from fishermen, independent observers and on-board video monitoring.

Simulation scenarios

The model is run for 30 years, starting in 2020, to estimate the dolphin population in 2050 under current dolphin protection measures and the level of protection recommended by the IUCN (Figure 2). A 'burn-in' period of 50 days is used to allow the dolphins to distribute themselves according to depth and distance from shore, matching the results of the most recent population surveys.

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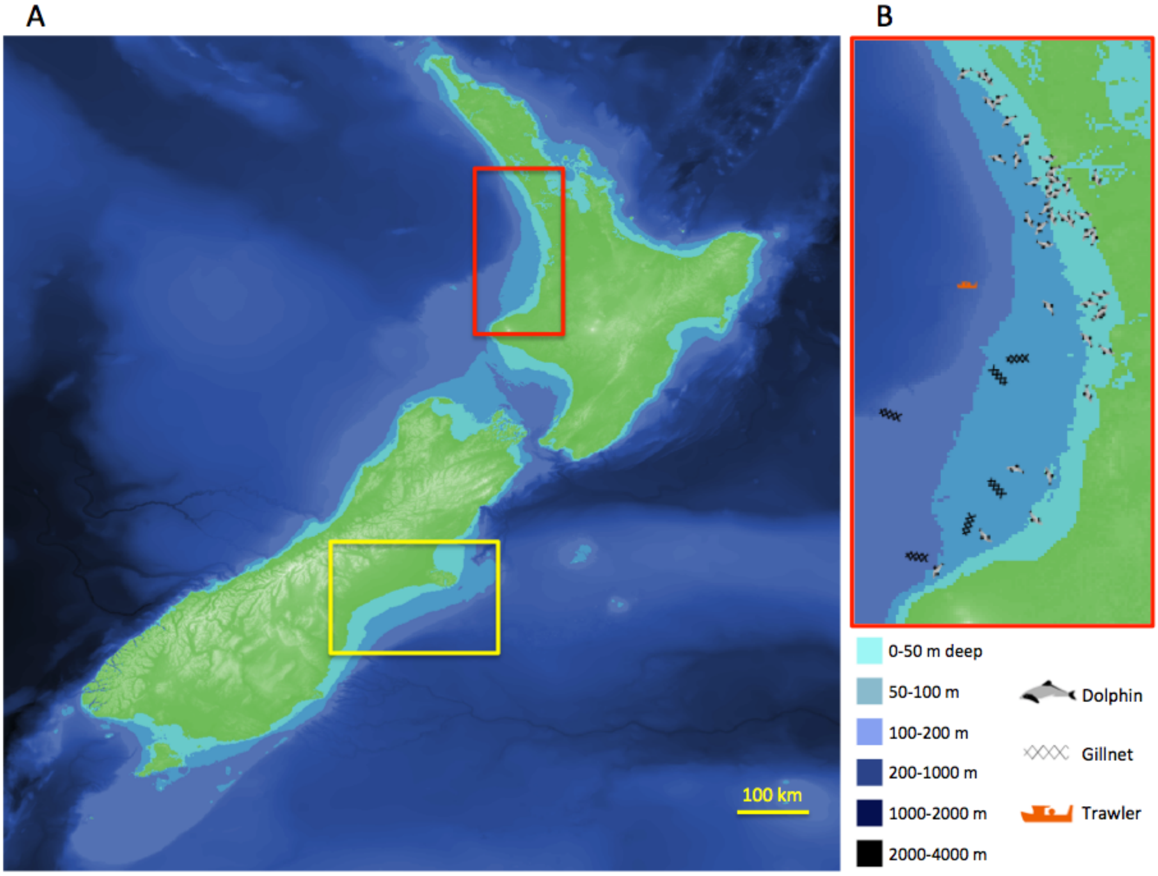

Figure 1. Map of model landscape, showing New Zealand's North and South Islands (Figure 1A). The red box shows a snapshot of the simulation model from part of the west coast of the North Island (Figure 1B), with realistic spatial distributions of dolphin, gillnet and trawler agents. The size of the dolphins, gillnets and trawlers has been exaggerated to make them visible on the map. The yellow box indicates the Banks Peninsula to Timaru area, where high observer coverage and high dolphin densities have resulted in all but two of the observed dolphin catches.

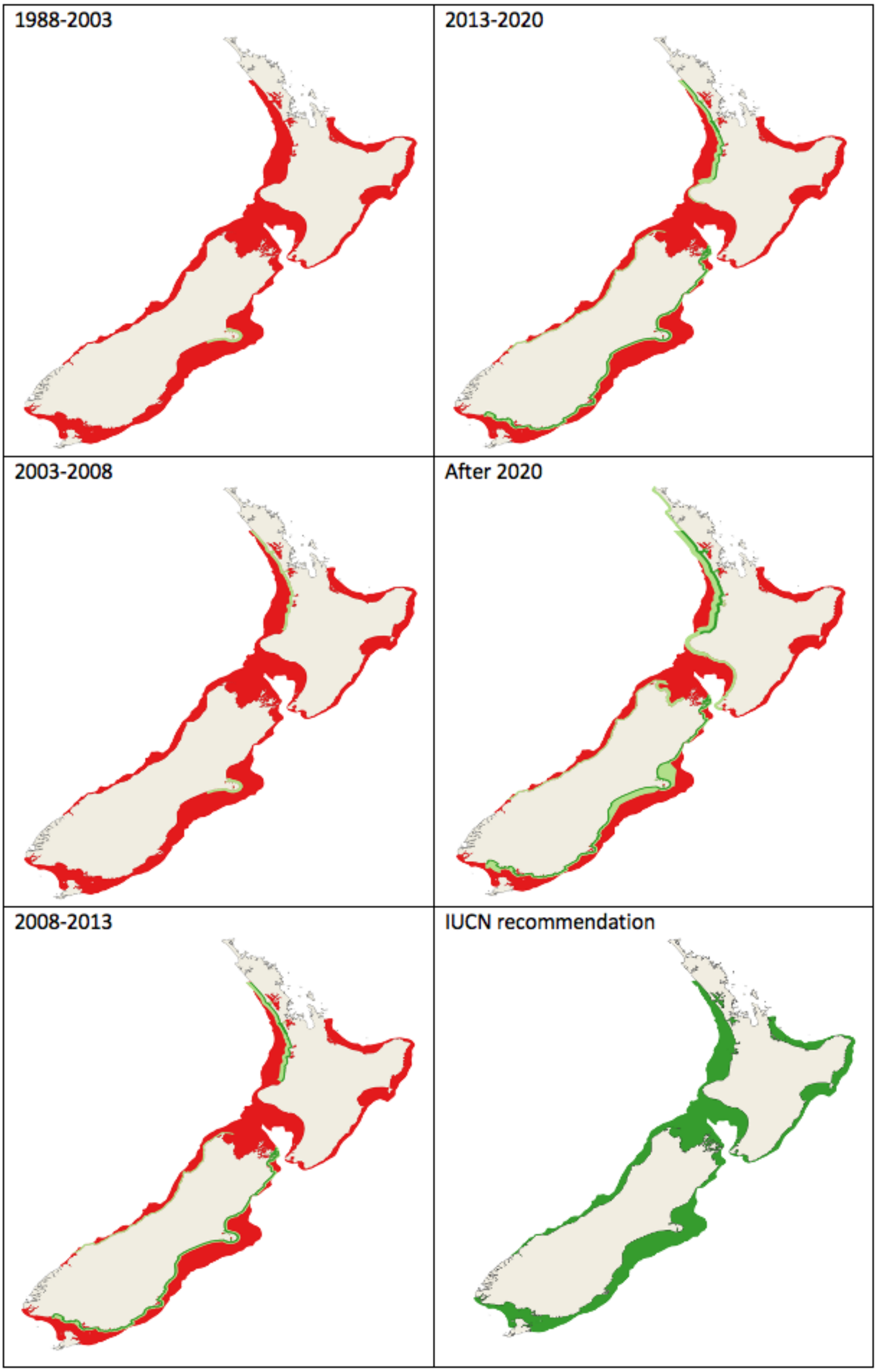

Figure 2: History of dolphin protection. The distribution of Hector's and Māui dolphin is indicated in red, areas where gillnets are banned in light green and areas where both gillnets and trawling are banned in dark green.

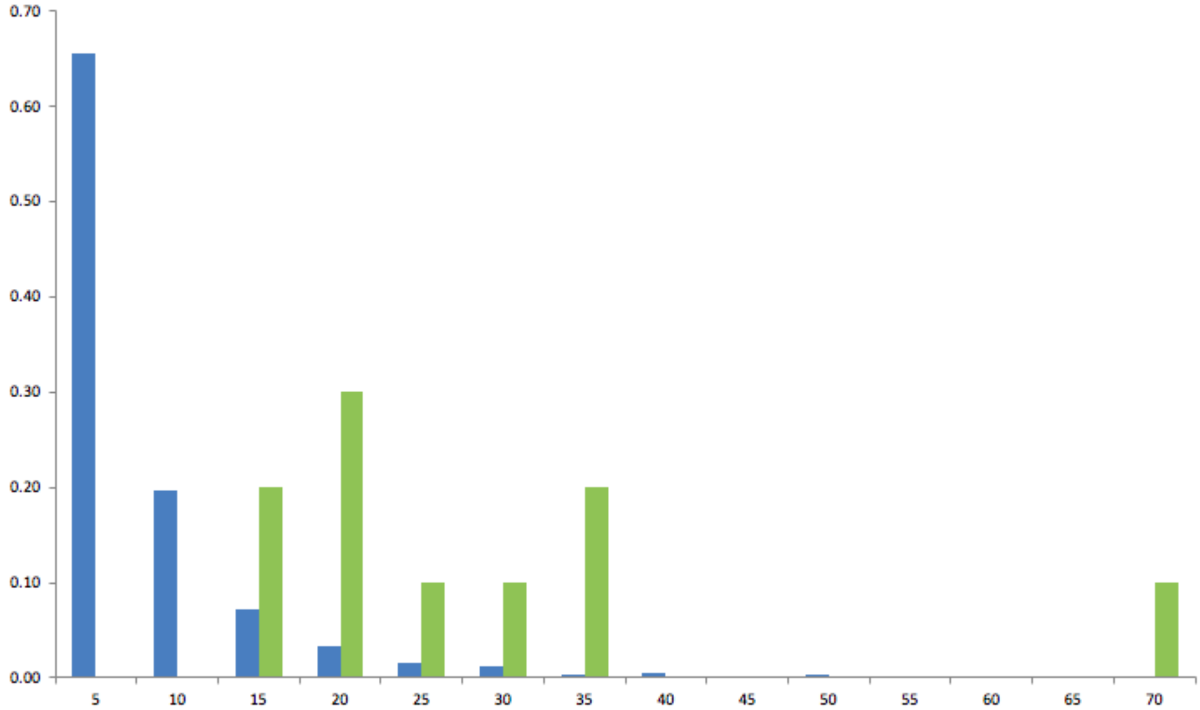

Figure 3: Group size of Hector's dolphins observed in the wild between 1991 and 2020 (blue bars, N=9,345), including dolphin groups observed following trawlers (green bars).

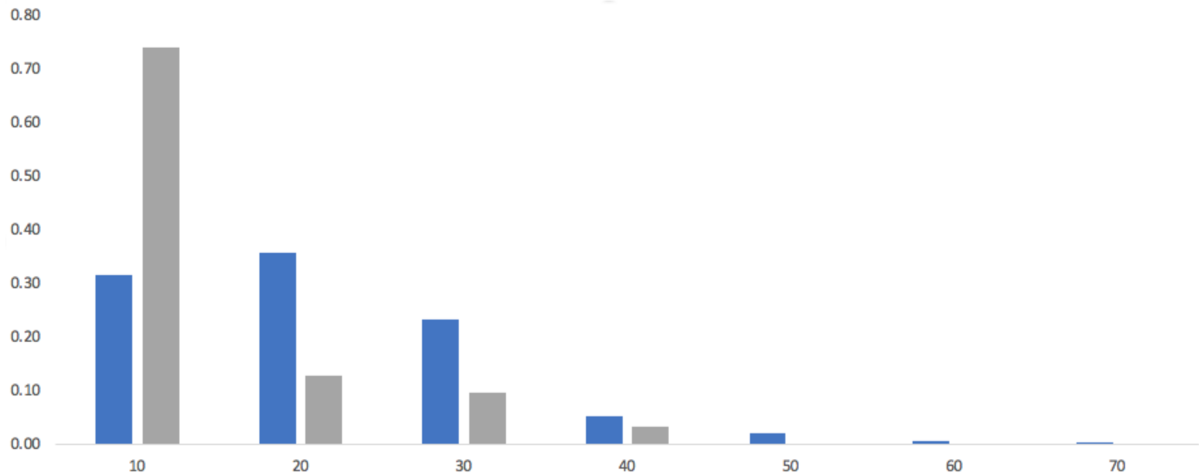

Figure 4: Distance covered (in km) by individual dolphins per day (grey bars) and by trawlers per trawl event (blue bars

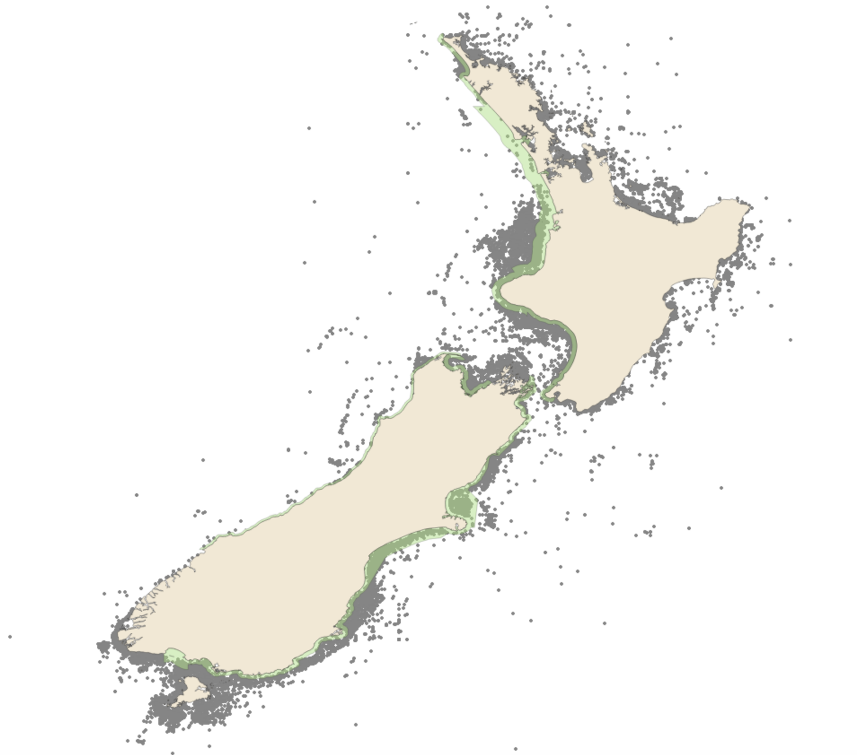

Figure 5: Gillnet fishing effort (grey) and current protection from gillnet fishing (green).

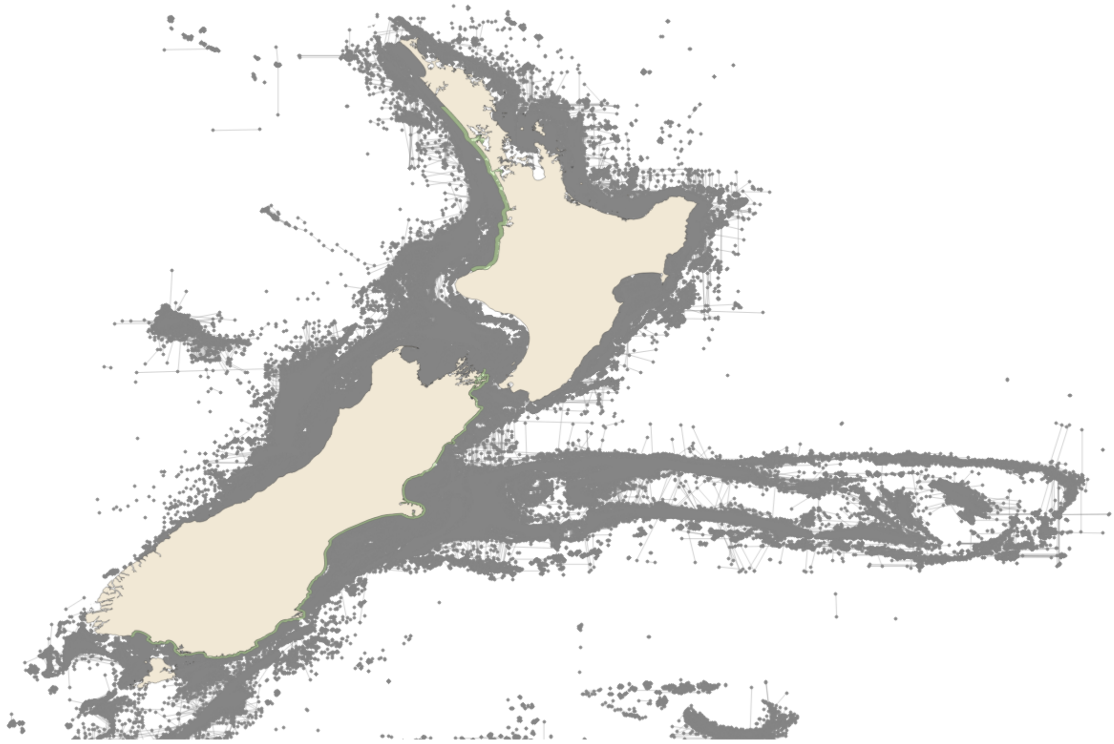

Figure 6: Trawl fishing effort (grey) and current protection from trawl fishing (green).

Figure 7: Trawlers followed by groups of dolphins, observed from research vessel. Dark green: Trawling and gillnets banned (shoreline to 2 nautical miles offshore); Light green: Gillnets banned; Yellow stars: Dolphin deaths in trawl nets (showing number of dolphins killed); Red lines: Trawlers operate inside and on the boundary of the area where trawling is banned, because the regulations allow continued trawling (with headline height < 1 m) inside the trawl ban area.