

**HABITAT USE THROUGHOUT A CHONDRICHTHYAN'S LIFE**

BY

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## ABSTRACT

Over the last few decades, much effort has been devoted towards evaluating and reducing bycatch in marine fisheries. There has been a particular focus on quantifying the risk to chondrichthyans, primarily because of their relatively high vulnerability to overfishing. A key part of risk assessment is evaluating the distributional overlap of the fish with the fisheries, where fish distribution is influenced by habitat use. I synthesised published observations of habitat use for different life history stages of chondrichthyans and hypothesised the associated catch composition in terms of fish sex, size, and maturity. I then searched for these catch compositions, and thereby locations, using New Zealand research vessel catch data. Results show that some life history stages and habitats for certain species can be identified, whereas others could not. Pupping ground criteria were met for *Callorhynchus milii* (ELE), *Hydrolagus novaezealandiae* (GSH), and *Hydrolagus bemisi* (GSP); nursery ground criteria were met for *Callorhynchus milii* (ELE), mating ground criteria were met for *Callorhynchus milii* (ELE), *Hydrolagus novaezealandiae* (GSH), *Hydrolagus bemisi* (GSP), and *Harriotta raleighana* (LCH); lek-like mating criteria were met for *Hydrolagus novaezealandiae* (GSH). For those life-history stage habitats not found, this may be because these are outside of the coverage of the data set (and likely also commercial fisheries), or because they do not actually exist for some chondrichthyans. On the basis of results, I propose to change the order of species in the New Zealand qualitative (Level 1) risk assessment, and rise the relative risk for *Hydrolagus bemisi* (GSP), given the species vulnerability of pupping grounds.

## Keywords

*Chondrichthyans; Biology; Ecology; Habitat use; Habitat; Bycatch; Conservation; Sharks; Skates; Rays; Chimaeras; Review*

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## CHAPTER 1: INTRODUCTION

The United Nations Food and Agriculture Organisation (FAO)’s International Plan of Action for the Conservation and Management of Sharks (IPOA-Sharks) recognizes that sharks are an important component in maintaining healthy ecosystems within the ocean (United States National Plan of Action for the Conservation and Management of Sharks 2001), and that these animals have certain biological characteristics that may make them vulnerable to fishing threats (e.g. slow maturation and low productivity; Kyne and Simpfendorfer, 2007). The primary goal of the IPOA-Sharks is “to ensure the conservation and management of sharks and their long-term sustainable use” (United States National Plan of Action for the Conservation and Management of Sharks 2001). The IPOA-Sharks advises members of the FAO to construct a National Plan of Action for the Conservation and Management of Sharks (NPOA-Sharks). This plan identified goals and objectives in the following areas: biodiversity and long-term viability of shark populations; utilisation, waste reduction and the elimination of shark finning; domestic engagement and partnerships; non-fishing threats; international engagement; research and information (United States National Plan of Action for the Conservation and Management of Sharks 2001).

Over-exploitation of fish stocks has been identified as the dominant direct driver of biodiversity loss in the marine environment (Russ, 1991; Jackson et al. 2001; Simpfendorfer and Kyne, 2009; Butchart et al. 2010). The failure of national fisheries management alone to protect fish stocks has led to increasing calls for the application of multilateral environmental agreements (MEAs), such as the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) and the Convention on the Conservation of Migratory Species of Wild Animals (CMS), to marine species.

The New Zealand NPOA Sharks (2013) recognizes that New Zealand (NZ) is home to at least 113<sup>1</sup> taxa of shark, where more than 70 have been documented in NZ fisheries. The term “shark” is exercised loosely in the NZ risk assessment, referring to all sharks, rays, skates, chimaeras and other members of the Class *Chondrichthyes*.

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<sup>1</sup> This number differs from that published in Francis & Lyon 2012 as that list (119 species) includes four species of Antarctic skates, and two species which have since been identified as species already on the list.

## **1.1 Risk assessment**

A risk assessment reviews species characteristics and stock status to ensure that appropriate management and protection are applied to a certain species. This allows for prioritisation of those species/stock where management measures are critical and also identifies those stocks where improvements to management measures are needed. In some instances, protection measures under multilateral environmental agreements might be warranted, or the need for such steps could be averted if prompt action is taken to address identified problems. Risk, in this context, is defined as: “Population-level risk, which is a function of impact and depends on the inherent biological or population-level characteristics of that population” (NPOA-Sharks 2013).

Risk assessment is increasingly recognised as an effective means of helping to manage natural resources (Conover and Munch, 2002; Hilborn, 1992; McConnaha and Paquet, 1996; Wissmar and Bisson, 2003). In recent years, risk assessment has been used to assess, for example, impacts of climate change and the ecological risk posed by fishing (Cotter et al. 2014). This means steps have been taken to understand and evaluate the impacts of climate change alongside what happens to the environment when an ecosystem is overfished and overexploited.

New Zealand adopted its first NPOA-Sharks in 2008, with its implementation reviewed in 2012. This review noted that eleven shark species managed under the Quota Management System (QMS) made up 90% of total shark catches from commercial fisheries. The QMS includes catch limits and enforced monitoring systems. Areas of fishery improvement identified by the NPOA-Sharks included a better utilisation of caught sharks, and a ban on all shark finning fisheries (minus one; the exception being for blue sharks, for which finning was scheduled to be eliminated no later than October 2016).

New Zealand then implemented a modified National Plan of Action for the Conservation and Management of Sharks (NPOA-Sharks 2013), setting directions for the period 2013 to 2018 (NPOA-Sharks 2013 will be reviewed in 2017 and revised in 2018). The NPOA-Sharks instituted a risk-based method to ranking management actions, to help ensure that utilisation of sharks is sustainable. The New Zealand Aquatic Environment and Biodiversity Report No. 157 itemised conclusions from the qualitative (Level 1) risk assessment (RA) workshop held in November 2014, where risks to all New Zealand Chondrichthyes from commercial fishing were evaluated (Ford et al. 2015).

The risk assessment conducted and described by Ford et al. (2015) was a form of Ecological Risk Assessment. Ecological Risk Assessment (ERA) is increasingly being used across a range of marine threats and habitats (Halpern et al. 2007; MacDiarmid et al. 2012; Cortés et al. 2014). Methodologies to assess risks from fisheries have been established and are generally organised into three categories (after Hobday et al. 2011):

- **Level 1:** Qualitative expert-established risk assessments used for the “data poor” fisheries, or to investigate higher risk species for a comprehensive assessment.
- **Level 2:** Semi-quantitative risk assessments, where more information/data has become available but is still not sufficient for a quantitative assessment.
- **Level 3:** Quantitative risk assessments, where there is enough data available to carry out a complete, quantitative assessment.

Generally for risk assessments, appropriate indicators of risk are identified, data are collected and analysed to calculate them, and the indicators compared against reference points or simply used to order species’ relative risk. Most ERAs done for New Zealand fisheries have been either Level 1 or 2. The scope of the Level 1 ERA was limited to commercial fishing threats on New Zealand Chondrichthyes, due to Chondrichthyes clearly being caught in fisheries, leading to better data existing on fishing-related threats (Francis and Lyon, 2013). The assessment focused on the last five years (2008-09 to 2012-13) so that it was relevant to the “present day” threats; a possible downside to this method is that researchers did not consider long-term threats or trends in stock status.

For New Zealand’s qualitative (Level 1) RA, a data compilation was achieved preceding the November 2014 workshop, allowing for the ensuing dialogue and assessments about risk to be as objective as possible (Ford et al. 2015), although data were sparse for many species. An expert panel scored the risk present to every species from commercial fishing; using fisheries data and available information on the specific taxon’s biological productivity, and risk. The qualitative RA used a modified Scale Intensity Consequence Analysis (SICA) approach (Hobday et al. 2011), which detailed the *intensity* and *effect* (the ecological consequence of the impact) of the fishery to the taxa on a scale of 1 to 6, where 1 was deemed low, and 6 was deemed high. The basis for the two scores for each taxon was recorded, and then they were multiplied together to get a total risk score (the maximum risk score generated was

21; possible maximum score was 36). Fishing intensity was scored for temporal and spatial subcomponents (estimated from catch quantities, maps of catch and range, and assessing the temporal nature of the fishery). Fishing effect was scored from management and compiled biological factors (where available) for all species.

In addition to the Ministry for Primary Industries (MPI) risk assessment (Ford et al. 2015), *TRAFFIC* (the wildlife trade monitoring network) was contracted to undertake the New Zealand M-Risk assessment review, completing the report in March 2014. An M-Risk assessment similarly identifies the species/stocks of sharks of potential concern and their relative level of concern. For sharks, M-Risk assessment includes a lot of variables: there are a number of shark species (approximately 112 species of sharks have been recorded from New Zealand waters) with many different lifestyles, differences in their market value for different body parts (like meat, oil, fins, cartilage), what body parts they use for sharks (like some sharks have both their fins and meat utilized but not their oil, some just have their fins were taken, etc.) and how to identify sharks once on the market (Fisheries Agency of Japan, 1999; Vannuccini, 1999; Yeung et al. 2000; Froese and Pauly, 2002; Clarke and Mosqueira, 2002). The *TRAFFIC* report ranked *Cetorhinus maximus*, *Dalatias licha*, *Lamna nasus*, *Isurus oxyrinchus*, *Mustelus lenticulatus* as “medium,” while rating *Notorynchus cepedianus*, *Carcharhinus brachyurus*, *Centrophorus squamosus*, *Squalus acanthias*, *Deania calcea* as “high.” Compared to Ford et al. 2015, this places *Mustelus lenticulatus* and *Dalatias licha* as lower risk and *Notorynchus cepedianus* and *Carcharhinus brachyurus* at higher risk.

New Zealand has broad monitoring, control, and supervision of fishing to make sure there is compliance with current management frameworks. In principle, the New Zealand fishery catch reports should be accurate. This is within New Zealand fisheries waters and New Zealand vessels fishing on the High Seas, from capture, through the point of landing, to a final destination (Ministry for Primary Industries). Monitoring management includes fishing permits and vessel registers, which has the vessel monitoring system and vessel/gear marking. There are also audits of licensed fish receivers, monitored unloads of fish and control of transshipment, information management and intelligence analysis, boarding and inspection by fishery officers at sea, aerial and surface surveillance. The measures allow analysis and comparison of data from a number of sources to confirm that fishers are complying with legal requirements. Under this system catch data are recorded within New Zealand’s EEZ and

Territorial Sea, and for New Zealand flagged vessels fishing on the High Seas that land their catch in New Zealand and elsewhere.

The data were reported for the three management classes of sharks: Quota Management System (QMS), Non-QMS, and Protected species. The stock status of the 11 QMS shark species are reviewed annually or as new information comes in. As QMS sharks may be targeted by fisheries, and tend to have relatively high catches (compared to most non-QMS species), it was anticipated that they would score relatively high in terms of intensity. Within the non-QMS class, species are managed either as open or limited access and can be subjected to individual conservation actions.

The outcome of the latest New Zealand Risk Assessment was new research based on these priorities (research underway). The RA also helped satisfy the expectations of NPOA-Sharks 2013 and IPOA-Sharks.

## **OBJECTIVES AND STRUCTURE OF THIS THESIS**

This thesis presents a method to assist evaluation of the impacts from fishing, habitat degradation, and resource loss facing Chondrichthyan populations. It should also be acknowledged that the open involvement of management and scientific experts, together with additional time to seek out and consider information on individual assessments, would undoubtedly result in more accurate assessments. It is intended that the following methodology will help this process and stimulate future work.

The overarching aim of this thesis was to improve Level 1 RA and, in particular, look at why some Chondrichthyan species that are commonly caught were not ranked high risk despite having characteristics that make them especially susceptible to overfishing. The following section in this chapter presents an extensive literature review of habitat use in Chondrichthyans, leading to hypotheses of how species use different habitats during certain life history stages, and what characterizes the catch composition from these locations. Chapter two applies the hypotheses developed in chapter one to an extensive scientific dataset for five chimaeras of specific interest for this thesis: *Callorhynchus milii* (MPI code ELE), *Hydrolagus novaezealandiae* (GSH), *Hydrolagus bemisi* (GSP), *Harriotta raleighana* (LCH), and *Rhinochimaera pacifica* (RCH). These species were chosen because they

cover a large range of depth (7 m – 1306 m), and had been noted as being abundant despite extensive fisheries (Ford et al., 2015), and they were of special interest to the Deepwater Group (who funded the scholarship for the MSc). This approach differs in that it develops hypotheses for characteristics of different habitat use, rather than “data mining” for patterns, and it therefore has a structured and scientific approach to determining shark habitats. Quantitative stock estimates are unavailable for all species (Ministry for Primary Industries, 2016). Chapter three will discuss the findings, and the implications for the risk facing these species.

## **1.2 Hypotheses of Habitat Use**

### **1.2.1 Introduction**

Sharks occur in all of the world’s oceans and in all habitats, including but not limited to, the deep-sea, oceanic, neritic, coastal regions and estuaries (Clark and von Schmidt, 1965; Lineaweaver and Backus, 1969; Castro 1993; Nakano and Nagasawa, 1996; Castro 2000). In an effort to properly manage and conserve sharks, the information regarding their habitat use and preference is important to consider when suggesting management strategies (Barker and Schluessel, 2005; Barnett et al. 2013; Dulvy et al. 2014). Habitat use, selection and preference affect population dynamics, interspecific and intraspecific interactions, ecosystem structure and biodiversity (Morris 2003).

Data on population structure, dispersal, habitat use and life history of many Chondrichthyans is crucial for implementing effective management efforts, and the lack of such information delays protection in all levels (Palsboll et al. 2007). In order to determine the home range of an animal and its habitat use patterns, the movements of the individual and the habitats where they occur must be obtained over a long enough period of time to be meaningful (i.e. at least two years, as it may change from year to year or season to season). Movement data can be obtained in many ways:

- a) Direct observation
- b) Relative catch rates
- c) Acoustic tracking and monitoring
- d) Satellite tracking

### 1.2.2 The Concept of Habitat

#### Habitat

In the most clear-cut definition, the habitat of an organism is the space where it resides (Odum 1971). Habitats can also be defined as the sum of the specific resources that are needed by organisms (Thomas 1979). These resources consist of sustenance, shelter, and other components needed by the individual for its survival and reproductive success (Leopold 1933). A habitat is species-specific, in that the components necessary for survival and reproduction are not the same for all species.

#### Habitat Use, Habitat Utilisation and Habitat Selection

*Habitat use* is defined as the habitats an individual or species frequents most often. This is also regarded as *habitat utilisation* or *habitat selection* in other literature (Ulrich et al. 2007; Morrissey and Gruber, 1993).

In order to describe habitat use, one must first determine an individual's home range, which was first developed in regards to terrestrial mammals (Burt 1943) and birds (Odum and Kuenzler, 1955). The definition of a home range has evolved over time. Burt (1943) originally defined the home range as "that area traversed by the individual in its normal activities of food gathering, mating and caring for its young." The home range does not encompass the area that the individual traverses during its lifetime, but where it normally resides.

However, Burt's definition left out those animals that did not care for their young, such as sharks. Cooper (1978) pointed this out, arguing that an individual may not use all portions of the home range equally. Several authors agreed, instead defining home range as the region that accounts for 95% (or some other percentage) of the space an individual utilises (e.g. Anderson 1982; Jennrich and Turner, 1969; Worton 1987). This definition and approach to a home range is known as *utilisation distribution* (UD).

Numerous studies of shark migrations and movement patterns have defined home range(s) and habitat use patterns through active and passive telemetry (e.g., Dawson and Starr, 2009; Heupel et. al 2004, 2006; Holland et. al 1993; McKibben and Nelson, 1986; Morrissey and Gruber, 1993a; Papastamatiou et. al 2010; Yeiser et al. 2008), although none actually specified whether habitats were chosen by preference.



## Habitat Preference

Hall et al. 1997 defines habitat preference as “the consequence of habitat selection, resulting in the disproportional use of some resources over others.” Note that this definition is different from how habitat selection was defined above; the review found literature sometimes lacked clarity in the use of these terms.

Some movements may be random. For example, a habitat that has an even spread of resources within it, will have random movement from the animals that inhabit it. However, if a habitat does not have an equal spread of resources, this movement is no longer random as it is related to the resources. This behavior may be explained by the optimal foraging theory (OFT), a model that aids in predicting how an individual animal acts while foraging for food. Although if successful their efforts culminate in feeding, the individual loses energy in the process of finding and handling the food. There are certain constraints animals face when making decisions (be it about foraging grounds or suitable habitat—which may be the same place); temporal constraints (the time it takes to find and then process the food), energetic constraints (metabolic cost of each activity- like foraging- versus time), processing constraints (if prey is too large for the animal to consume) and perhaps even cognitive constraints (possible limit to learning/memory) (Werner et al. 1983). OFT can encompass the ideas of balancing feeding against predator avoidance, reproductive need and other life history pressures.

### 1.2.3 A Refined Habitat Terminology

The above terms (bold) are often used interchangeably in ecological literature, causing confusion in what these terms actually refer to. Because of the varied use of terms, for this thesis the terms were defined as follows:

**Habitat:** The sum of the particular resources needed by an organism in order to survive (Thomas 1979). These resources include shelter, sustenance, and other specific considerations required by a species for its survival and reproductive success (Leopold 1933).

**Habitat Selection:** An active behavioral process which combines instinctive and learned decisions made by an organism about what habitat it would use at different scales of the environment during certain life stages (Hutto 1985). Interacting influences include, but are not limited to foraging, competition, territoriality, shelter, and predation risk.

**Habitat Use:** The way an organism uses the physical and biological aspects in a habitat (a consequence of habitat selection). This habitat may be used for various life history traits.

**Habitat Preference:** Habitat preference is the consequence of habitat selection and habitat use, leading to a disproportional use of some resources and areas in a habitat over others. One of the well-known mechanisms underlying habitat preference is the OFT.

**Habitat Availability:** Habitat availability is the accessibility of physical and biological components of a habitat to organisms (i.e. tides can frequently change habitat availability).

**Critical Habitat:** Critical habitat is a legal term defining the physical and/or biological qualities vital to the protection and management of a species (U.S. Fish and Wildlife Service 1988).

With these above definitions put in place, habitat use and habitat preference are consequences of habitat selection (e.g. a shark will not occur in all of the habitats within its range; instead, it is more likely to have specific habitats in which it spends most of its time). You can liken this to the process of buying a house. For example, when buying your home, you choose its location (habitat selection) based on several factors. You will use the area surrounding your home (habitat use), but will have your favourite spots within that area (habitat preference). In this instance, a shark will not occur in all of the habitats within its range; instead, it is more likely to have specific habitats in which it spends most of its time.

#### 1.2.4 Distinguishing Patterns from Chance

Yet, what if *habitat preference* was not at play? If the ranges were randomly arranged within a certain geographical region that lacked environmental gradients, they would overlap in the middle of said constrained area (e.g. latitude, altitude or depth), creating a “mid-domain” peak of species occurrence. The *mid-domain effect* (MDE) applied to species richness (biodiversity) suggests that observed apparent pattern and structure in an environment can occur by chance (i.e. those areas highest in diversity can be just by chance). A review of 21 MDE studies revealed a substantial signature of MDE in natural patterns (Colwell et al. 2004).

Within an area of habitat use, an animal’s movement could be (i) random, (ii) stratified (OFT) or (iii) stratified random (random within a selected area). The concern here is really about recognising when a pattern (ii) or (iii) is true, or just an artefact. This is important in this thesis because I am potentially

interpreting samples as being representative of structure (ii or iii), when they might just occur by chance.

The mid-domain effect (Colwell and Hurtt, 1994; Colwell and Lees, 2000a; Jetz and Rahbek, 2001) has been controversial in both its understanding and its use but the insight it has brought has been valuable and it highlights the importance of recognising chance events as such (Bokma and Mönkkönen, 2000; Brown 2001; Koleff and Gaston, 2001; Hawkins and Diniz - Filho, 2002; Laurie and Silander, 2002; Zapata et al. 2003). MDE models are null models; they intentionally omit a feature or mechanism of (possible) influence, offering a control to compare against with actual data sets (Harvey et al. 1983; Colwell and Winkler, 1984; Gotelli and Graves, 1996; Gotelli 2001). Null models aren't new to ecological sciences (Gotelli and Graves, 1996), and are a well-established, but highly debated, tool (Gotelli 2001). MDE models are not all-encompassing. Most published studies that use MDE models are based on endemic species (species restricted to a particular domain; Colwell and Lees 2000a). This may be a possible limitation of the current application of MDE models (Koleff and Gaston, 2001; Rahbek and Graves, 2001; Whittaker et al. 2001; Hawkins and Diniz-Filho, 2002; Laurie and Silander, 2002). While empirical backing for the MDE is usually weak, it is varied. Habitat preference may be at play, but MDE predictions should not be disregarded, and instead, equally evaluated with other statistical explanations.

It should also be taken into account that animals can very occasionally wander outside of their home range, as this range could be spatially or temporally inconsistent. This may be due to the home range not fulfilling the needs of the animal (e.g. they could migrate out of the 'typical' home range due to the resources present in another habitat for a short amount of time). OFT may be at play here; as mentioned earlier, searching for a particular resource requires energy and time, even though obtaining sustenance provides energy if successful. It may also be an innate "need to wander" (i.e. dispersal phase).

This thesis is not using null models, but instead relies on repeated observations as criteria to show structure. In other words, recognition of structure should rely on more than just passing observation in a specific area once or twice throughout a study. Repeated observations are required to infer pattern and structure, otherwise these rare occurrences could have transpired by chance.

### **1.2.5 Habitats and Life History Stages**

Throughout a Chondrichthyans' life, habitat selection changes. Habitat selection can be broken up into four key areas: pupping/egg laying areas, nurseries (offshore or inshore), foraging grounds, and mating grounds. These key life history phases and associated habitat characteristics are summarized in **Table 1**.

**Table 1. Chondrichthyan habitat characteristics and life history, and reported (cited) habitat types and composition in respect to life cycle.** Characteristics written in italics are *presumptions* from the literature while characteristics not in italics are cited in the text.

<b>LIFE STAGE AREA</b>	<b>LIFE STAGE COMPOSITION</b>	<b>CHARACTERISTICS [relative]</b>	<b>REPORTED LOCATIONS</b>
<b>Pupping grounds</b>	<i>Neonates, large females (gravid or recently spent)</i>	Near nursery grounds	Mudflats, bay, estuary, marsh wetlands
<b>Egg laying area</b>	<i>Eggs, neonates, large females (gravid or recently spent), no males</i>	Well-ventilated and sheltered locations near nursery grounds	Elevated colonies of octocorals, gorgonians, cold seeps, canyon heads and edges
<b>Nursery (inshore)</b>	<i>Neonates; relatively high density of juveniles; possible adults (low density)</i>	Shallow, sheltered area with warm, productive, water	Estuary, mangroves, lagoon, bayou, coral reef
<b>Nursery (offshore)</b>	<i>Neonates; relatively high density of juveniles; possible adults (low density)</i>	Shallower water than adults, productive water	Continental shelves, seamounts and islands, open water
<b>Mating ground</b>	<i>Mature females and males (about 1:1 sex ratio), possible sub-adults</i>	No consistent pattern. <i>Spatially and temporally persistent location</i>	Mangroves, bay, estuaries, coral reef, coastal waters, open water
<b>Mating ground: lek</b>	<i>High density of mature males, lesser density of mature females</i>	Little known information. <i>Spatially and temporally persistent location.</i>	Anywhere
<b>Mating ground: aggregation</b>	<i>Primarily mature females and males, sub-adults possibly present as well</i>	Daytime, disperse at night. <i>Spatially and temporally persistent location</i>	Anywhere
<b>Food aggregation with possible mating</b>	<i>Primarily mature females and males, sub-adults possibly present as well</i>	Wherever there is food in large quantities. <i>Spatially and temporally persistent location in regards to prey</i>	Anywhere
<b>Exclusive foraging ground</b>	<i>Mature females and males, sub-adults possibly present</i>	Wherever there is food in large quantities	No consistent pattern

### 1.2.6 Pupping Grounds: Lack of a Definition

An exact definition of a pupping ground does not seem to exist; at present, all pupping areas are considered nursery areas (Heupel et al. 2007; Merson and Pratt, 2001). One might refer to an area as a pupping ground based on the observation of only sexually mature females (meaning late-development pups or post-partum) being in the region. Most scientists think of pupping grounds as primary nurseries, not really differentiating between the two as distinct regions (Merson and Pratt Jr., 2001; Parsons and Hoffmayer, 2007; Rechisky and Wetherbee, 2003; Heupel et al. 2007). With a stricter definition, some pupping areas may be nurseries, but not all will fall under the Heupel et al. (2007) criteria for a nursery ground (see: Nurseries).

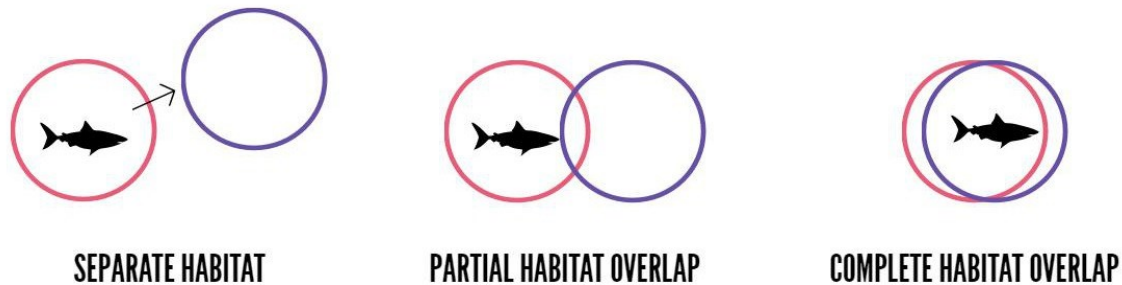
Many shark species use discrete regions throughout their life cycle for purposes that include parturition (Meek 1916) and early growth and development (Castro 1993), yet these locations remain unknown for the most part. Anecdotal evidence suggests that Rajids and other oviparous species of Chondrichthyans have distinct egg-laying grounds and require a suitable substratum for their eggs. For example, concentrations of egg capsules of the deep-water skate *Bathyraja richardsoni* were discovered in a specific environmental niche of well-oxygenated waters between 4.20 and 4.55° C, and a second type of egg capsule (possibly skate *Dipturus* sp.) was recorded exclusively amongst the reef-building stony coral *Solenosmilia variabilis* (Henry et al. 2016). An unknown species of *Scyliorhinid* catshark was reported to deposit eggs at well-ventilated and sheltered locations assumed to increase their chances at survival while decreasing predation risk (Etnoyer and Warrenchuk, 2007). Able and Flescher (1991) recorded 300 egg cases of *Scyliorhinus rotifer* fixed to hydroids (*Eudendrium* sp.) in bottom trawls, proposing that the complex habitats formed by hydroids may also serve as a nursery once the eggs hatched. *Scyliorhinus canicula* was reported to deposit their eggs on multiple upright structures (e.g. erect sponges, hydroids, soft corals and bryozoans; Ellis and Shackley, 1997). Other examples of well-ventilated habitats/locations with eggs found include elevated colonies of octocorals and gorgonians (Etnoyer and Warrenchuk, 2007), canyon heads (Hoff 2010), edges (Love et al. 2008) and old-seep habitats with tubeworm colonies (Treude et al. 2011).

Treude et al. (2011) found abundant catshark (Chondrichthyes: *Scyliorhinidae*) and skate (Chondrichthyes: *Rajidae*) egg capsules in recently-made seeps (i.e. the Mediterranean Sea and South-East Pacific Ocean), suggesting that deep-water elasmobranchs may use them for egg-laying sites in various locations worldwide. Treude et al. (2011) also included the collection of fossilised shark egg

capsules from a 35 million-year-old seep deposit in the North American Cascadia accretionary wedge, lending to the idea this association is not new.

Gravid females of some shark species embark on long-distance migrations to an assumed protected habitat to deliver their pups away from adult sharks, possibly for a lower risk of cannibalism (Feldheim et al. 2002; Ebert 2002; Morrissey and Gruber, 1993; Snelson et al. 1984). The migration of these pregnant females to inshore pupping grounds has been detailed in oceanic white-tip shark (*Carcharhinus longimanus*: Backus et al. 1956), leopard sharks (*Triakis semifasciata*: Ebert and Ebert, 2005), Caribbean sharpnose sharks (*Rhizoprionodon porosus*: Mattos et al. 2001) and spurdog (*Squalus acanthias*: Hickling 1930). My definition for pupping is therefore a region where sexually mature females give birth and/or possibly lay eggs, without sexually mature males in the area (**Table 1**). This areas composition is typically made up of gravid or “recently spent” females, and young neonates. Therefore, this may or may not be the same habitat as “nursery” grounds.

The relationship between adult habitat and pupping grounds can be summarized in the following scale (**Fig. 1**). The scale has three categories that Chondrichthyans may fall into: “**separate habitat**,” “**partial habitat overlap**,” and “**complete habitat overlap**.”



**Figure 1.** A summary of habitats relating mature and juvenile Chondrichthyans to pupping grounds (**Table 1**): separate habitat, partial habitat overlap, and complete habitat overlap. Pink denotes mature female home range; purple symbolize pupping grounds.

**Separate habitat** is when a mature female’s home range is completely different from pupping grounds, requiring a migration to a specific location to give birth/lay eggs, and temporary residence in that area for that purpose only. The female shark home range (95% of time) and pupping ground do not overlap. Sharks in this category might travel long distances to give birth, like sandbar sharks (*Carcharhinus plumbeus*; Damon 1996; Merson 1998; McCandless et al. 2007; Grubbs and Musick, 2007; Grubbs et al. 2007).

**Partial habitat overlap** is when a mature female's home range slightly overlaps with pupping grounds. These Chondrichthyans do not have to travel far to a specific area to lay eggs/give birth. Sharks in this category include the lemon shark (*Negaprion brevirostris*; Feldheim et al. 2002; Henderson et al. 2010; McKenzie, 2013).

**Complete habitat overlap** is when a mature female's home range almost completely overlaps with pupping grounds. Some areas are habitats that mature females or small sharks can go but the other cannot (i.e. size). Sharks in this category include blue sharks (*Prionace glauca*; Smale 1991; Yokota and Lessa, 2006), seal sharks (*Dalatias licha*; Francis 1998) and nurse sharks (*Ginglymostoma cirratum*; Carrier 1985; Carrier and Pratt, 1993; Carrier and Pratt, 1998).

### 1.2.7 Nurseries

Nurseries are of particular research interest due to their assumed importance in the shark's life history, with numerous studies defining a nursery (definition: habitat use patterns in regard to young sharks) and stressing their importance in conservation (Bass, 1978; Branstetter, 1990; Castro, 1993; Clarke, 1971; Duncan and Holland, 2006; McCandless et al. 2007; Morrissey and Gruber, 1993a; Simpfendorfer and Milward, 1993; Springer, 1967; Kinney and Simpfendorfer, 2009). The majority of studies regarding Chondrichthyan habitat use focus on the easier to access shallow, coastal nurseries of *Carcharhinid* and *Sphyrnid* species (Simpfendorfer and Heupel, 2004; Chin et al. 2016).

Heupel et al (2007) provided a guideline in determining whether an area was a shark nursery or not, focusing on three criteria: (1) [newborn or individuals <1 yr old] sharks are more commonly encountered in the area than in another area, (2) sharks have a tendency to remain or return for extended periods (i.e. site fidelity), (3) the area or habitat is repeatedly used over years. This last criterion is site fidelity, the continued return and/or continued use to a particular area (Switzer 1993), and has been observed in some sharks, including scalloped hammerhead sharks and white sharks (Klimley and Nelson 1984; Domeier and Nasby-Lucas 2007; Weng et al. 2008).

Inshore habitats (i.e. mudflats, bays, estuaries, marsh wetlands, mangroves, lagoons, bayous and shallow coral reefs) are used by a number of shark species including, but not limited to, lemon sharks (*Negaprion brevirostris*; Feldheim, Gruber and Ashley, 2002), bull sharks (*Carcharhinus leucas*; Castro 1993),



blacktip sharks (*Carcharhinus limbatus*; Keeney et al. 2005), Mexican horn shark (*Heterodontus francisci*; Castro 2011), smooth dogfish (*Mustelus canis*; Castro 1993), rig (*Mustelus lenticulatus*; Francis et al. 2012), school shark (*Galeorhinus galeus*; Francis et al. 2012), elephant fish (*Callorhynchus milii*; Francis et al. 2012) and several rays (Francis et al. 2012). Whether these are nurseries or inshore pupping areas is unclear. These near shore habitats are frequently used as nurseries (Kinney and Simpfendorfer, 2009; Yates et al. 2010), providing a haven for juvenile sharks, with a lower predation risk and shallow, warmer waters that tend to be more productive than deeper regions (Beck et al. 2001). Here, juvenile elasmobranchs have fast growth rates (Beck et al. 2001), and reduced predation risk (Morrissey and Gruber, 1993; Heupel and Hueter, 2002; Rechisky and Wetherbee, 2003; Grubbs and Musick, 2007), while they expand their range within the nursery and better their foraging capabilities (Gislason et al. 2010). Juvenile sharks may also leave one recognised nursery for another: inshore nursery habitats in tropical and subtropical regions may be occupied year-round (Yokota and Lessa, 2006) or seasonally (e.g. Simpfendorfer and Milward, 1993) while year-round occupancy in temperate regions is harder due to temperature fluctuations (Musick and Colvocoresses, 1986).

Whilst inshore nurseries seem to be common, offshore nurseries are rarely described. Vandeperre et al. (2014) tracked 34 blue sharks of different life stages for up to 952 days and, unlike studies that suggested juvenile regions to be inshore from adult regions (Smale, 1991; Yokota and Lessa, 2006; Aires, Ferreira and Pereira, 2008a), provided evidence for existence of a central North Atlantic and oceanic nursery; this may suggest flexibility in a shark's life history. It is still unknown what benefits are provided by oceanic nurseries, as they may not have habitat complexity that leads to obvious value.

Vandeperre et al. (2014) study tested the guidelines proposed by Heupel et al. (2007) on blue sharks, and revealed that blue sharks are locally abundant across years (Aires, Ferreira and Pereira, 2008a) and that individuals tend to remain and return to the same area, meeting the nursery ground criteria proposed by Heupel et al. (2007). No other nursery grounds for offshore species have been identified or described to my knowledge and their occurrence, locations and characteristics remain poorly understood.

My definition for a Chondrichthyan nursery does not aim to contradict Heupel et al. (2007); instead, it includes in its definition that there should be a relatively high density of juveniles and low density of adults, and if adults do occur, they are more likely large females (**Table 1**).

## Benefits of a Nursery

Benefits of nurseries are generally presumed; objective measurement of actual benefits is lacking (this would require translocation). The presumed benefits of nursery grounds have been reported in several papers (Kinney and Simpfendorfer, 2009; Duncan and Holland, 2006; Knip et al. 2010). Grubbs' (2001) manual telemetry data suggested larger, shallower and warmer nighttime activity spaces for juvenile sandbar sharks than their daytime activity spaces. This supports Sims' (2003) hypothesis that sharks seek habitats that maximise net energy gain and that these two times may differ in pros and cons.

Branstetter (1990) suggested that there was a complex trade-off relationship between requirements of different life stages. In addition to the benefits of nursery areas, the size-at-birth, rate of growth, time to maturity, litter size and frequency of breeding were factors to take into account as potential trade-offs. Branstetter went on to suggest food as an unlikely influential factor of whether or not a Chondrichthyan needs a nursery (as nurseries are typically within high productivity environments, allowing ample sustenance for juvenile sharks) and instead argued predation risk as the greatest concern for young sharks. He identified two types of nursery areas: "The nursery grounds can be categorised by their degree of exposure to potential predators. Some are 'protected,' because they are in areas infrequently inhabited by adult sharks, while others are very 'unprotected,' because they are located in habitats occupied by adults (Branstetter 1990, pg. 18).

The varying degrees of protection provided by a nursery area can vary between species. Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*) are a smaller-sized species that is born offshore, and juveniles move to coastal bays in spring (Carlson 2002; Parsons and Hoffmayer, 2005), exposing these sharks to large predators. Based on the small size of their pups, and the idea proposed above, one would assume these pups would reside in a specific type of inshore, protected habitat rather than a wide use of open environments, to avoid predation. This smaller-sized coastal shark has a relatively productive life history strategy (i.e. rapid growth, early maturity, annual reproduction) and relatively high rate of population growth (see Cortés 2002 for a review) when compared to other shark species. Therefore, the benefits of nursery areas for these species may be limited. However, for those smaller-sized species with slow growth and late maturity, the opposite may be true. For example, the life history of school sharks (*Galeorhinus galeus*) includes a small size at birth (33 - 35 cm, Compagno 1984), slow growth and late maturity (ca. 8 yr, Moulton et al. 1992). Due to these life history characteristics, this species probably benefits from the use of a protected nursery area with high prey density and low

predation risk. Olsen (1954) has identified numerous areas for this species in eastern Tasmania and Victoria, Australia with high densities of school shark pups that are presumed nurseries.

Branstetter (1990) introduced the concept that scientists should not assume all sharks actually have nursery areas, and instead, that some species may do without this often assumed “vital” component of a shark’s life history (Heupel et al. 2007; see Heithaus, 2007 for the use of theory in designing studies of essential habitat of shark nurseries). The lack of nursery grounds tradeoff might occur when species are born at relatively large body sizes and grow faster relative to those in protected nurseries. With more research into the multifaceted trade-offs of “nursery” vs “no nursery” lifestyle of these animals, we can perhaps begin to piece together what life characteristics can predict a certain lifestyle.

Nursery benefits may also extend to mature sharks. Castro (1993) discusses that nurseries may involve more than one type of habitat, as different ontogenetic stages may encompass multiple habitats. The coastal waters of Bulls Bay, South Carolina and the nearby barrier islands are a shallow nursery for a number of sharks: blacknose (*C. acronotus*), spinner (*C. brevipinna*), finetooth (*C. isodon*), blacktip (*C. limbatus*), sandbar (*C. plumbeus*), dusky (*C. obscurus*), Atlantic sharpnose (*Rhizoprionodon terraenovae*), scalloped hammerhead (*Sphyrna lewini*), and smooth dogfish sharks (*Mustelus canis*). Based on landing data from early summer, the female populations of the finetooth, sandbar, and blacktip sharks were divided into two groups: mature females with mating bites and ripe oocytes, and gravid females who were about to give birth (note that earlier we defined this component of a population as representing a pupping ground). Gillnet captures revealed that gravid females were in shallower water than mating females, caught at deeper depths. Castro (1993) concludes that in some species, only half of the population (those about to give birth) will enter a nursery (pupping ground) in a given year (i.e. non-reproductive females will not do the migration and remain in the feeding ground). This is an example of where the definition between pupping and nursery ground is not clear in the literature, but where pupping and nursery grounds also have at least partial overlap.

### **Departing the Nursery and Dispersal**

Literature points to many reasons as to what triggers a shark to make the decision to leave a nursery: tidal changes (Wetherbee et al. 2007), temperature tolerance (Merriner et al. 1976; Snelson and Williams 1984; Musick and Colvocoresses 1986; Francis 1988), salinity, turbidity, dissolved oxygen levels (Blaber and Blaber 1980; Blaber and Cyrus 1992), growing body size (Bouskila et al. 1998). Intuitively, it is possible that their larger body size no longer allows for the successful hunting of

smaller prey within the complex habitats of a nursery ground (e.g. Morrissey & Gruber 1993b). This, coupled with a change in dietary and energetic requirements, may prompt them to leave their safe rearing habitats to have greater access to food (McNab 1963). A larger body size can help lower the risk of predation outside of the nursery, making the trade-off worth it (Gislason et al. 2010).

The exit of juveniles from a nursery could be considered a dispersal phase. Bouskila et al. (1998) suggested that juveniles can synchronise their departure, reducing their risk through dilution of predation. This may also allow for an earlier exit from the nursery; what benefits leaving a nursery early or the individual gains once away from the group is unknown. It is also unknown if females and males tend to disperse with their respective sex (i.e. females leaving first) or mixed (i.e. females and males together), although Klimley (1984) noted that female scalloped hammerhead sharks, *Sphyrna lewini*, left their inshore nursery areas at a younger age than their male counterparts. Overall, the influences beneath the selection of nursery habitats and their eventual departure are not well known. Most literature is just a description of location, not functional benefits possibly provided by nurseries.

In summary, most species of Chondrichthyans often have nurseries, but it is possible they are not distinct areas; this depends on the life history trade-offs in regards to the species. Nurseries are most often inshore, but might be offshore (little is known about offshore nurseries). However, this may be a “detection bias” as those inshore tend to be easier to study.

### **1.2.8 Expanding ranges: Movement, Migration, Dispersal and Ontogenetic Shifts**

The terms “movement”, “migration” and “dispersal” are often confused and necessitate clarification. In this thesis, the definitions of Koehn and Crook (2013) are used. They are:

#### **Movement**

The change in location of an animal; should be used when not discussing a specific kind of movement (i.e. migration and dispersal).

#### **Migration**

The movement of an animal that involves most of the population with some regularity and movement from one habitat/environment to another (examples of sharks are lacking but e.g. upstream movement of Golden perch to spawn followed by downstream drift of larvae; Llewellyn 2014).

## Dispersal

Movement of an animal from areas where they are concentrated to areas where they are less concentrated (examples of sharks are lacking but e.g. postglacial fish dispersal from Mississippi refuge to Mackenzie River basin; Rempel and Smith, 1998).

The differing scales and purposes of fish movements are summarised in **Table 2** below (modified after Koehn and Crook, 2013).

**Table 2.** Varying degrees, descriptions and purpose of movements in animals (modified after Koehn and Crook, 2013).

<b>Movement</b>	<b>Description</b>	<b>Purpose</b>
<b>Micro-scale</b>	Short, non-sustained bursts	Escape from predators & prey capture.
<b>Meso-scale</b>	Short term but sustained, within normal home range	Feeding, avoidance of local poor conditions, diel movements & spawning.
<b>Macro-scale</b>	Prolonged, long-term, large scale movements between habitats	Migrations, exploration, feeding, dispersal, spawning & avoidance of larger scale poor conditions.
<b>Direction</b>		
<b>Longitudinal</b>	Upstream and downstream	Migrations, spawning, feeding & genetic mixing.
<b>Lateral</b>	In channel, on to floodplains, in/out of lake littoral zones	Dispersal, recolonisation, feeding & larval rearing.

Once a shark matures to adulthood, defining a home range for the individual becomes challenging, as adult habitats often span thousands of square kilometres (Sundstrom et al. 2001). Various coastal and pelagic shark adult habitats may include an entire ocean basin, making observations of ontogenetic shifts in movements and patterns of habitat use hard to evaluate (Weng et al. 2007; Weng et al. 2008; Gore et al. 2008; Jorgensen et al. 2009; Brunnschweiler et al. 2009).

## Ontogenetic Shifts

Ontogenetic shifts in an individual, especially its diet, are common among the vertebrate taxa (Fishelson et al. 1987; McCormick 1998; Lind and Welsh 1994; Herrel and O'Reilly 2006; Page et al. 2005; Price and Grant 1984; Kitowski 2003), including Chondrichthyans (e.g. Jackson et al. 2004; Wetherbee and Cortes, 2004; Afonso and Hazin, 2015).

The changes that occur as an individual grows are due to a number of factors, including but not limited to, changes in food requirement, changing predation risk (increase in size, but also learned avoidance behaviours), and competition from conspecifics and other species. Lemon sharks undergo an ontogenetic shift in regards to home range expansion, with juveniles showing strong site fidelity and movement between tidal refuges, while adults have a wider range (Gruber et al. 1988; Morrissey and Gruber 1993b; Sundstrom 2001; Wetherbee et al. 2007; Chapman et al. 2009). Sundstrom (2001) looked at 20 lemon sharks (*Negaprion brevirostris*) and three species of rays and how food, water temperature, bottom substrate and magnetic gradient played a part in their movement patterns, concluding that lemon sharks do in fact exhibit not only innate homing skills but experience ontogenetic shifts in habitat selection and behavior. Morrissey and Gruber (1993a) found that juvenile lemon sharks selected shallow waters where temperatures were above 30°C, which served to maintain optimal metabolic performance while avoiding predators.

A study of bat rays (*Myliobatus californica*), leopard sharks (*Triakis semifasciata*) and smooth hound sharks (*Mustelis henlei*) in California found that their movements and distributions were also affected by temperature, as well as salinity (Hopkins and Cech 2003). Likewise, juvenile blacktip sharks expand their home range over months due to changes in environmental conditions or ontogenetic changes in behaviour (Heupel and Hueter 2001; Heupel et al. 2004, Heupel & Simpfendorfer 2005a). Salinity might affect the movement and distribution of bonnethead (Ubeda et al. 2009) and bull sharks (Simpfendorfer et al. 2005) in a Florida estuary, although temperature (Simpfendorfer et al. 2005; Heupel and Simpfendorfer 2008), water flow (Heupel and Simpfendorfer 2008; McCord and Lamberth 2009) and dissolved oxygen also appear to be important (Heithaus et al. 2009a). Studies have shown these types of changes in other species, such as sandbar sharks (Grubbs 2001; Grubbs and Musick, 2007; Grubbs et al. 2007), smalltooth sawfish (Simpfendorfer 2005), and basking sharks (Shepard et al. 2006). Understanding these changes will help develop effective conservation management strategies. The importance of habitat use studies has increased, and as such, these types of studies should continue. Scientists need to define and understand essential fish habitats for commercially fished species and critical habitats for endangered species in order to propose effective conservation management strategies.

Simpfendorfer et al. (2005) examined longline surveys in three estuarine habitats in south-west Florida, where mean length of immature bull sharks (*Carcharhinus leucas*) was significantly different between each of these areas, suggesting size-based habitat partitioning suggesting ontogenetic shifts. Habitat

partitioning may reduce intraspecific predation, and therefore increase the survival of the neonates present. Simpfendorfer (2005) studied immature smalltooth sawfish (*Pristis pectinata*), observing they were dependent on shallow, sand and mud bank habitats (<2 m deep), often not leaving water <30 cm deep. Adults, however, are known to travel in waters up to 100 m deep (National Marine Fisheries Service, 2009). Ontogenetic shifts should be expected in many species, as they seem to be ubiquitous. This is consistent with the ideas of “nurseries.”

### 1.2.9 Mature Chondrichthyans and Sexual Segregation

Since the 1960's, reports of sexual segregation in sharks, whether observed or suspected, have increased (e.g.: *Prionace glauca*: Pratt 1979; Stevens 1976; Bullis 1967; Springer 1967; *Sphyrna lewini*: Klimley 1985; *Carcharhinus amblyrhynchos*: McKibben and Nelson, 1986; *Carcharias taurus*: Gilmore et al. 1983; *Sphyrna tiburo*: Myrberg and Gruber, 1974). Yet, the causes of sexual segregation have never been investigated in any species, although the possible explanations have been discussed: differences in swimming abilities, dietary inclinations, lack of violent behavior between similar-sized sharks, or migration of gravid females to nursery grounds (Klimley 1987; Springer 1967). There are about 900 species of Chondrichthyans, among which sexual segregation is believed to be a common characteristic (Springer, 1967). In the Sims (2005) review of sexual segregation among sharks, 38 species demonstrated some degree of sexual segregation.

The first indication of possible sexual segregation in elasmobranchs came from commercial fisheries, where an imbalanced sex ratio was observed in trawl catches of female thornback ray *Raja clavata* (Day 1884). Fulton (1890, 1903) found a similar bias in sex ratio in the Scottish landings of *Rajiformes* in thornback ray (65.7% female), the sandy ray, *Leucoraja circularis* (61.7% female), and the common skate, *Dipturus batis* (51.3% female). Unequal sex ratios were also reported in landings of Canadian *Rajiformes* (Craigie 1927): females dominated most landings including for the winter skate (*L. ocellata*; 61%), thorny skate (*A. radiata*; 60%), barndoor skate (*Dipturus laevis*; 65%) and the little skate (*Leucoraja erinacea*; 55%). This can possibly indicate biased sex ratios in that particular area, or that one sex is more catchable than the other (e.g. males are smaller than females and therefore can get out of the net easier). Nevertheless, the repeated observations suggest a pattern of sexual segregation.

Ford (1921) observed male dominated landings of smoothhound, *Mustelus vulgaris*, in the western English Channel inshore fisheries off Plymouth, United Kingdom. Yet, in the autumn landings of the

spurdog, *Squalus acanthias*, females dominated (up to 92%). Variability in dominant catch (female vs male during certain times of the year) would suggest spatial and temporal sex ratio bias, rather than net selectivity. Such unequal ratios were also seen in the Pacific dogfish, *Squalus suckleyi*, with the dominating sex varying between catch location and season (Craigie 1927). Steven (1933) recorded thornback rays during their fishing season (January-March), with females dominating inshore areas throughout the season, but declining towards the end of the season. It was here that male numbers began to increase, suggesting a male migration inshore or a female migration offshore. The Plymouth investigation (Ford 1921) also revealed an inshore sex-specific migration, with lesser spotted dogfish (*Scyliorhinus canicula*) males dominating winter catches (65%) and females dominating in the summer (58%). These biased migrations could be same-sex individuals aggregating in preferred habitat rather than in other available habitats (geographical sexual aggregation; Backus et al. 1956) or individuals schooling with those of similar size and sex (behavioural aggregation; Backus et al. 1956).

Sexual segregation is not restricted to just mature individuals; Klimley (1984) noted that female scalloped hammerhead sharks, *Sphyrna lewini*, left their inshore nursery areas at a younger age than their male counterparts. This earlier offshore migration results in an increased intake of pelagic prey, as deduced from the observation of larger stomach content masses in females than in males of the same or similar size. Dietary differences amongst sexes is not just seen in juveniles: sex distinctions in the diet blue sharks, *Prionace glauca*, have been understood to result from sex-specific inclinations to certain foraging locations (McCord and Campana, 2003). However, by studying catches of individual vessels, Ford (1921) and Steven (1933) identified that catches of immature individuals had sex ratios of approximately equal proportions (1:1). Segregation by age is also an accepted general feature of shark populations (Springer 1967) and may also be apparent in the fishery catches. It is thought that schools of active shark species are assorted by size, with similar-sized individuals swimming at similar paces (Wardle et. al 1996).

### **Behavioural Segregation**

Ford (1921) discovered that 92% of spurdog (*Squalus acanthias*) in November were mature females, presenting an imbalanced and varied sex ratio of landings. Ford (1921) inferred that this sexual segregation was due to *S. acanthias* schooling with individuals of similar size and sex, which has been termed 'behavioural aggregation' (Backus et al. 1956). The spurdog (*Squalus acanthias*) is known for its large schools, making it an easy target for commercial fisheries (Compagno, 1984). This sort of segregation can be applied to pregnant females specifically; Wolf Rock, Australia is the only known



site where female *Carcharias taurus* segregate and aggregate during pregnancy (Bansemer and Bennett, 2009).

### **Geographical Segregation**

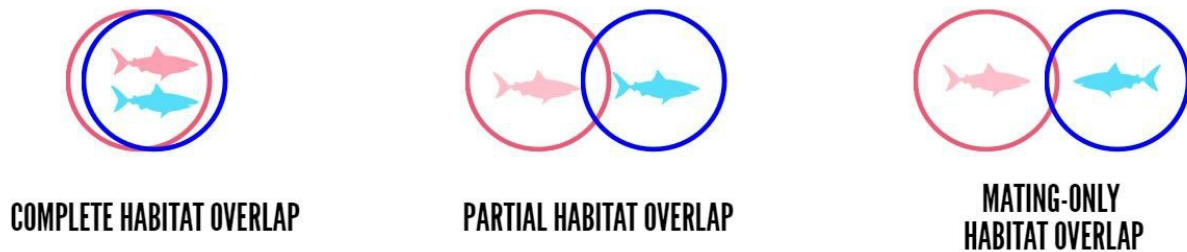
As demonstrated by Ford (1921) and Steven (1933) in thornbacks and lesser spotted dogfish, geographical segregation in elasmobranchs is often temporal in nature: for example, male cownose rays, *Rhinoptera bonasus*, greatly exceeded female numbers in Chesapeake Bay from June-July, which is when gravid females come in and dominate from late July-September (Smith and Merriner, 1987). This temporal geographic segregation is frequently depicted by seasonal patterns of mature females into shallower, often warmer, waters. Landings of *G. galeus* in the California region demonstrated that catch make-up varied by area as well as depth, with females appearing in shallower waters than their counterparts (Ripley 1946).

### **Temperature: A Significant Sexual Segregation Cause**

An environmental cue that may influence habitat selection of the sexes is temperature. Temperature has been correlated with the movement of the spurdog (*Squalus acanthias*; Shepherd et al. 2002), specifically their yearly offshore/inshore migrations. The falling coastal water temperatures were correlated with a move to offshore (Garrison 2000), implying that the spurdog were seeking out a habitat with ideal temperatures. Grey reef sharks, *Carcharhinus amblyrhynchos*, establish female-only groups in the shallow lagoons of Johnston Atoll in the Central Pacific Ocean, where the water temperatures were 1–2° C warmer than the open ocean, and sexual segregation was highest during the warmer hours of the day (Economakis and Lobel, 1998). Sexual segregation in white sharks, *Carcharodon carcharias*, at the Neptune Islands, South Australia, may be another example of how influential temperature is, as males were observed more during the winter, spring and summer, with the highest number of sightings being during September when water temperatures were lowest (males were observed in the temperature range of 14.3–17.8° C; Robbins 2007). Females, on the other hand, were mostly seen during autumn when water temperatures were highest (within the temperature range of 15.7–18.1° C) (Robbins 2007). Some studies have suggested temperature as the key driver in seasonal/temporal patterns of sexual segregation (Hight and Low, 2007; Speed et al. 2012). These areas with suitable thermal environments may promote residential behaviour in some species.

### 1.2.10 Adult Shark Scenarios

The degree of sexual segregation is summarized in terms of habitat overlap in **Figure 2**.



**Figure 2.** Summary of sexually mature female and male habitats in regards to each other (**Table 1**). Pink denotes mature female home range and mature female shark, blue symbolizes mature male home range and mature male shark.

The “**complete habitat overlap**” of sexes scenario describes populations that are mixed year-round (e.g. catches/observations often 50:50 sex ratio). For example nurse sharks, *Ginglymostoma cirratum*, in the Dry Tortugas, Florida, USA (Saville et al. 2002). Some areas are habitats that mature females or mature male sharks can go but the other cannot. No other literature examples of 50:50 sex ratio populations were found during this review.

The “**partial habitat overlap**” of sexes scenario implies that the two home ranges do overlap (e.g. feeding, mating) but sexes will tend to have distinct home ranges. For example, scalloped hammerhead shark, *Sphyrna lewini*, (Klimley 1987) dogfish, *Scyliorhinus canicula*, (Sims et al. 2001) nurse shark, *Ginglymostoma cirratum*, (Pratt and Carrier 2001) whale shark, *Rhincodon typus*, (Clingham et al. 2016). This scenario also implies that neither sex “migrates” very far, nor to a specific region, to mate. For example, Pratt and Carrier (2001) studied sex-specific philopatry in adult nurse sharks (*Ginglymostoma cirratum*) using tagging methods to identify reproductive males and females in the Dry Tortugas, Florida, U.S.A., and found that adult males visited the study site every year, with three specific males dominating the area, whereas individual females visited the study site to mate every other year.

The last scenario, “**mating-only habitat overlap**,” is where mature female and male home ranges only overlap during times of copulation and in a specific location. For example, lek-like mating system in great white sharks (Jorgensen et al. 2012). The rest of the time, these two sexes tend to have separate home ranges. No other examples of this home range arrangement were found during this literature review.

The “mating-only habitat overlap” does not imply that same sex individuals will always overlap, only that different sex individuals will not overlap. However, for those same sex individuals that do overlap, territorial behavior could be possible. Tagging has shown relative site-fidelity attachment in some species (Carraro and Gladstone, 2005; Heupel et al. 2010; Lowe et al. 2006; Skomal and Benz, 2004; Dudgeon et al. 2013), but no literature exists specifically on territorial behavior. It may be that any seen warning displays may be directed at the human observer as much as the potential rival.

The summary also takes into account that mature female sharks may show different patterns of movement depending on whether they are pregnant or are resting, and in this case sharks do not always fall into one category. Because of this potential complexity, we consider adult grounds in more detail below, and we will define what we consider mating grounds, and their subsets.

We might expect sex biases in catches to be normal. These biases might be random, but if influenced by underlying conditions of life history tradeoffs, then they would be systematic.

### **1.2.11 Aggregation of Adults**

#### **Aggregation Definition**

None of the literature defined how many individuals make up an aggregation. Yet, many sharks do aggregate at some point in their life history, resulting in a relatively high density of a particular species, sex, or size class at a specific site, including large predators (>4m; Weng et al. 2007), planktivores (Sims and Merrett, 1997; Meekan et al. 2006), coastal sharks (Klimley and Nelson, 1981; Dudley et al. 2005; Heupel and Simpfendorfer, 2005) and coral reef sharks (Stevens 1984; McKibben and Nelson, 1986; Gruber et al. 1988; Economakis and Lobel, 1998, Smith and Pollard, 1999; Pratt and Carrier, 2001; Whitney et al. 2004; Hight and Lowe, 2007).

Aggregations may occur during the daytime, dispersing at night, and in both adult and juveniles for some species (e.g. Klimley and Nelson, 1984; Duncan and Holland, 2006). Aggregations tend to be attributable to site fidelity, ‘refuging’ behavior, predator avoidance (e.g. Klimley and Nelson, 1984; Economakis and Lobel, 1998; Hight and Lowe, 2007; Wetherbee et al. 2007), and can involve multiple species at the same time (e.g. McKibben and Nelson, 1986; Gruber et al. 1988).

The reasons for aggregations are poorly understood, but several functions have been proposed including 1) *courtship/mate selection* (Carrier et al. 1994; McKibben and Nelson, 1986), 2) *reproduction* (Olsen 1954; Jensen 1965; Kenney 1968; Klimley and Nelson, 1981; Carrier et al. 1994), 3) *energy conservation* (Klimley and Nelson, 1984), 4) *social interactions* (Klimley 1985) and 5) *refuge from predators or aggressive males* (McKibben and Nelson, 1986). The definition of an aggregation with mating intentions in this thesis is a catch composition of sexually mature sharks, possibly with sub-adults present, at a spatially and temporally persistent location (**Table 1**).

### **Mating Ground Definition**

None of the literature reviewed clearly defined what constituted a mating ground. In this thesis we use the following definition: a spatially and temporally persistent location where sexually mature females and males are present in equal proportions (1:1 sex ratio), and where sub-adults may be present but juveniles are not. Reported mating grounds did not show a consistent pattern in habitat, and occurred in estuaries, bays, coral reefs, coastal waters or open water. Use of mating grounds might also be variable, as sperm storage has been recorded in some species of sharks (*Lamna nasus*, *Rhizoprionodon terraenovae* and *Carcharhinus obscurus*; Pratt 1993), and allows for sharks to not be present at mating grounds every year.

### **Possible Mating Ground: Food Aggregation Definition**

Prey aggregations may take place due to interactions between the physical and biological oceanography of the region. For example, Graham et al. (2006) reported that, since 1999, a number of professionals (researchers, tour operators, etc.) on a Mesoamerican Barrier Reef have observed a seasonal feeding aggregation of whale shark, where highest shark numbers coincided with the near-surface spawning aggregation of snappers *Lutjanus cyanopterus* and *L. jocu* following the full moon in March through June. Mating had not actually been seen (Graham et al. 2006), but feeding aggregations like these could allow for systematic overlap of the sexes. A recent publication regarding whale sharks in St. Helena (Clingham et al. 2016), provided preliminary evidence (observations) that whale sharks use the habitats around St. Helena for both feeding and mating, thereby suggesting a combined food and mating aggregation ground.

In this thesis, the definition of a food aggregation with possible mating is a relatively high density of Chondrichthyans with a catch composition of primarily mature females and males (some sub-adults

present), in a spatially and temporally persistent location, associated with high densities of prey (**Table 1**).

### **Possible Mating Ground: Lek Definition**

A lek is loosely defined as a group of males that aggregate to engage in displays in hopes that a female finds them as a suitable mate (Fiske 1998). Although most prevalent in avian species, Höglund and Alatalo (1995) provide a review of lekking in animals, including 97 bird species, 13 mammal species, 11 amphibian species, 72 insect species, and 21 fish species. Lek-like mating has been observed in the following fish families: *Synodontidae* (Donaldson 1990), *Balistidae* (Gladstone 1994), *Gadidae* (Windle and Rose 2007), *Salmonidae* (Figenschou et al. 2004), *Cichlidae* (McKaye 1983), *Cyprinidae* (Wedekind 1996), *Sparidae*, *Labridae*, *Scaridae*, *Acanthuridae*, *Poeciliidae*, *Characidae* and *Centrarchidae* (Loiselle and Barlow 1978); it is likely a main reproductive component for internally reproducing species (Höglund and Alatalo 1995).

There is no known parental care in Chondrichthyans. Sexual selection is directed by two means: the female's mate choice, whereby females compare males and choose those with the most attractive phenotype, or through demonstrations of endurance (Andersson 1994; Jennions and Petrie 1997). The requirements of lek systems, were outlined by Bradbury (1981): 1) *no male paternal care* 2) *males are aggregated in an arena where females come solely for the purposes of mating* 3) *there is no unique resource to females except the males themselves* and, 4) *female mate choice*. In this thesis, my definition of a lek follows Bradbury (1981), and adds that a lek must be in a spatially and temporally persistent location, in order for the sexes to successfully meet (**Table 1**).

Endurance rivalry simply means increasing the individual's time spent in a mating location, which in turn increases chances of mating (Andersson and Iwasa 1996). This boils down to the ability of an individual to outlast competition in a mating location, and by extension, encourages female attention. This sort of endurance display can be seen in the numerous *Manta alfredi* breaching events and courtship displays documented by Marshall and Bennett (2010). In their study, Mozambique, particularly the Inhambane coast from Zavora in the south to the Bazaruto Archipelago in the north, emerged as an important aggregation area. During October and January, 90.6% of breaching activity took place within 48 hours of observed courtship displays, mating events or fresh mating scars (Marshall and Bennett 2010). Courtship displays were variable in length, but all tended to include the

following: a) close pursuits of females, b) faster than average swimming speeds, and c) multiple males performing one after another in view of the females (Marshall and Bennett 2010). Although this suggests endurance, with possible female male choice, lek-like mating systems have never been described among elasmobranchs. In fact, multiple paternity in Chondrichthyans has been found (Gubili et al. 2012; Byrne and Avise, 2012) and argues against lek-like mating.

Therefore, despite the reported lek behavior in other internally reproducing fish species, this form of reproductive behaviour does not seem to occur in Chondrichthyans. Therefore, we would not *a priori* expect to find leks.

### **1.2.12 Other Chondrichthyan Movements**

#### **Philopatry**

Philopatry (Greek for "home-loving") is defined as an animal's natural tendency to return to a home area, natal site, or other assumed site (Mayr 1963); site fidelity is a type of philopatry. Most philopatry research has focused on the homing behavior of migratory birds, yet several animals display some degree of philopatric behavior. Philopatric inclinations can vary between and within species; special cases include natal philopatry (returning to their birthplace to breed and/or give birth) and sex-specific philopatry (one sex is more philopatric) (Weatherhead et al. 1994; Greenwood 1980). Philopatry also suggests that while each animal has a "home habitat," this habitat may not be the same for every animal.

Evidence of philopatry in Chondrichthyans is still weak, as there are several challenges when trying to find compelling evidence of philopatry (Hueter 1998). As some species are highly mobile, they cannot be studied with orthodox tagging or tracking methodology, and their inherently low level of genetic variation reduces the efficiency of genetic tools (Heist 1999; Feldheim et al. 2001; Smith 1986; Keeney et al. 2003; Stow et al. 2006; MacDonald 1988).

If certain Chondrichthyans do display philopatry, instead of roaming throughout their overall home range, the impact that habitat alteration and fishery removal could have on their population(s) and stock(s) may be profound. If they are philopatric in regards to regions of such as mating area or nursery ground, active fisheries in those sections can remove individual animals of population importance (i.e. sexually mature sharks, gravid females or pups). This could have a dramatic effect on the relative

abundance of the species in a localized area, wiping out a specific part of their range or area required by particular life stages. The former is known as localized stock depletion, and Walker (1998) reviews this for sharks, with present day examples in the shark meshing program in South Africa (Dudley 2002) and Australian commercial fisheries (Walker 1998). Ecological changes affecting distribution may give the appearance of localized depletion in highly migratory species, as was seen in basking sharks off Ireland where a long-term zooplankton (total copepod) decline caused a downward trend in shark catches because fewer copepods (their food source) occurred near the surface (Sims and Reid 2002).

However, sharks that have no philopatry tendencies, which are highly migratory and have a large home range, may be immune to localized stock depletion. Simpfendorfer (1992) did not observe an apparent decrease in the tiger shark (*Galeocerdo cuvier*) population size in the Townsville AU area as a result of long-term fishing pressure (protective meshing programme). This may be due to the high mixing of movements of tiger sharks. This type of behavior, may explain why certain shark populations (including New Zealand chimaeras considered in this thesis) have apparently not declined as much as other species exposed to the same fisheries (Baum et al. 2003; O'Driscoll et al. 2011; Carlson et al. 2012).

### **Small Scale Movements: Foraging Within a Small Area**

Prey distribution within a habitat can be regulated by a number of biotic and abiotic factors, resulting in patchiness and, therefore, small-scale foraging patterns in predators (Steele 1976; Benfield et al. 1998). Studies have shown that small spatial areas (<10km) are preferentially inhabited by basking sharks, showing selective foraging behavior in a particular zooplankton patch (Sims and Quayle, 1998). In the seagrass ecosystem of Shark Bay, Western AU, tiger sharks (*Galeocerdo cuvier*) undergo small-scale foraging movements for both benthic and air-breathing prey, where their distribution is influenced by prey availability (Heithaus et al. 2000). Another example are rig sharks (*Mustelus lenticulatus*) in Porirua Harbour (25 km north of Wellington) move from one side of the harbour (mud sediment) to the other half (a fast flowing channel with little if any prey) (Lyon 2015).

## Large Scale Movements: Diel Vertical Migrations (DVM)

The ocean is a 3D habitat. There are three proposed hypotheses to account for diel vertical migrations (DVM) found in several fish species, including sharks (Nelson et al. 1997; West and Stevens, 2001; Sims et al. 2005; Weng and Block, 2004; Wilson et al. 2005; Rowat and Gore, 2007): bioenergetic efficiency, foraging opportunity and predator avoidance (Scheuerell and Schindler, 2003). Bioenergetic efficiency proposes that species make vertical migrations to select temperature for optimum growth (Brett, 1971; Wurtsbaugh and Neverman, 1988). This predicts that fish feed on the abundant prey on the surface at night, and move to deeper, cooler waters to rest and digest their meal. The foraging opportunity hypothesis proposes that fish follow spatio-temporal changes in prey abundance to maximize hunting opportunities, lending to higher overall growth (Narver, 1970; Levy 1990). The predator avoidance hypothesis proposes fish move vertically up and down the water column in response to avoid/reduce predation (Clark and Levy, 1998; Scheuerell and Schindler, 2003).

Sims et al. (2006) observed male dogfish (*Scyliorhinus canicula*) undertaking normal DVM (a nocturnal ascent) up submarine slopes into prey-rich water above the thermocline, within a small home range of about 100 x 100 m, finding activity levels were higher at night, and fewer vertical movements occurred during the daytime. This study indicated that these dogfish were foraging in the warmer water temperatures and resting in the colder depths. A thermal election trial revealed dogfish avoided warmer water, even when associated with ample prey (Sims et al. 2006). Males in an aquarium exhibited the same preference, which could possibly lower energy cost by a little over four percent (4%) (Sims et al. 2006).

Diel vertical migrations have also been observed in the megamouth shark (*Megachasma pelagios*; Nelson et al., 1997), the school shark (*Galeorhinus galeus*; West and Stevens, 2001), the basking shark (Sims et al., 2005), the whale shark (Wilson et al. 2006; Rowat and Gore, 2007) and the bigeye thresher shark (Weng and Block, 2004). Nelson et al. (1997) showed a megamouth shark displaying strong DVM when acoustically tracked off of southern California, exhibiting shallow nighttime and deep daytime dives anywhere from 20 m to 160 m. West and Stevens (2001) studied school sharks in southern Australia using archival tags that found they ascended the water column at night. Sims et al. (2005) studied basking sharks that exhibited normal DVM in deep, well-stratified waters but conducted reverse DVM (dusk descent, dawn ascent) in shallow, inner-shelf regions. Wilson et al. (2006) observed 19 whale sharks that performed frequent DVM and crepuscular descent, while Rowat and Gore (2007) suggested geo-strophic currents as an influence to whale shark DVM patterns. Weng and



Block (2004) studied two bigeye thresher shark movements, noting large temperature changes associated with DVM.

Vertical migrations are to be expected. This could bias the catch data if fisheries have a depth and diel pattern also.

### **Large Scale Movements: Open Oceanic Foraging**

It can be assumed that oceanic sharks, those that spend the majority of their time in open waters feed on a range of trophic level prey, allowing them to have adaptive foraging opportunities and behaviour adjusted for prey species and circumstance. Examples of oceanic sharks include, but are not limited to, bigeye thresher (*Alopias superciliosus*), blue (*Prionace glauca*), dusky (*Carcharhinus obscurus*), longfin mako (*Isurus paucus*), shortfin mako (*Isurus oxyrinchus*), night (*Carcharhinus signatus*), oceanic whitetip (*Carcharhinus longimanus*), porbeagle (*Lamna nasus*), sandbar (*Carcharhinus plumbeus*), scalloped hammerhead (*Sphyrna lewini*), silky (*Carcharhinus falciformis*), and tiger (*Galeocerdo cuvier*) (Cortés, 2000; Hazin et al. 2000; Cortés, 2002; Dulvy et al. 2008).

The diet of these species can be variable, indicating adaptive foraging, and is cause for higher risk to oceanic sharks in pelagic long lines (e.g. Beerkircher et al., 2002, Diaz and Serafy, 2005, Morgan and Burgess, 2007 and Morgan and Carlson, 2010).

### **Summary**

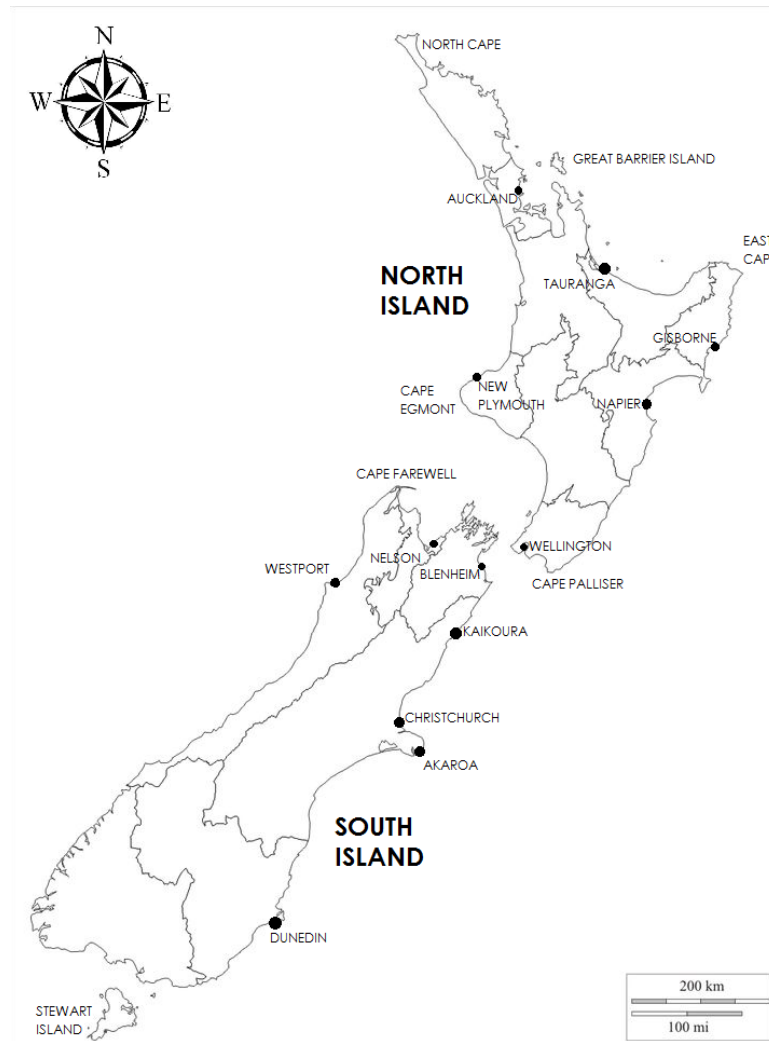
Expected characteristics of shark habitat use are variable, depending on the life history stage you are considering (**Table 1**). Nurseries, pupping grounds and mating grounds are likely to be found in most species whereas leks are unlikely. Inshore nurseries are the best studied, with lemon sharks being the most cited animal. Offshore nurseries are the least studied, with only blue sharks being studied. The explicit foraging aggregation, mating aggregation, and foraging and combined mating aggregation, are also likely to varying extents, but may sometimes be difficult to distinguish.

## CHAPTER 2: ANALYSIS FOR CHIMAERAS

### 2.1 METHODS

#### 2.1.1 Study Area

New Zealand is an archipelago of islands in the western South Pacific Ocean, with an Exclusive Economic Zone (EEZ) of almost 4.2 million km<sup>2</sup> (Gordon et al. 2010), making it the fifth largest EEZ in the world (MacDiarmid 2007). New Zealand has two main islands, the North Island and the South Island (**Fig 3**), separated by the Cook Strait, and numerous smaller outlying islands.



**Figure 3.** The New Zealand terrestrial region with names of a few cities and names of important oceanic features.

### *Islands and Bathymetry of Importance*

The Chatham Islands consist of 10 islands within a 40 km radius, at the eastern end of Chatham Rise close to the Subtropical Convergence (for a comprehensive review of the currents around New Zealand, consult Chiswell et al. 2015). This joining of warm and cool waters produces an area on the Chatham Rise that is high in biological productivity (O'Driscoll et al. 2011).

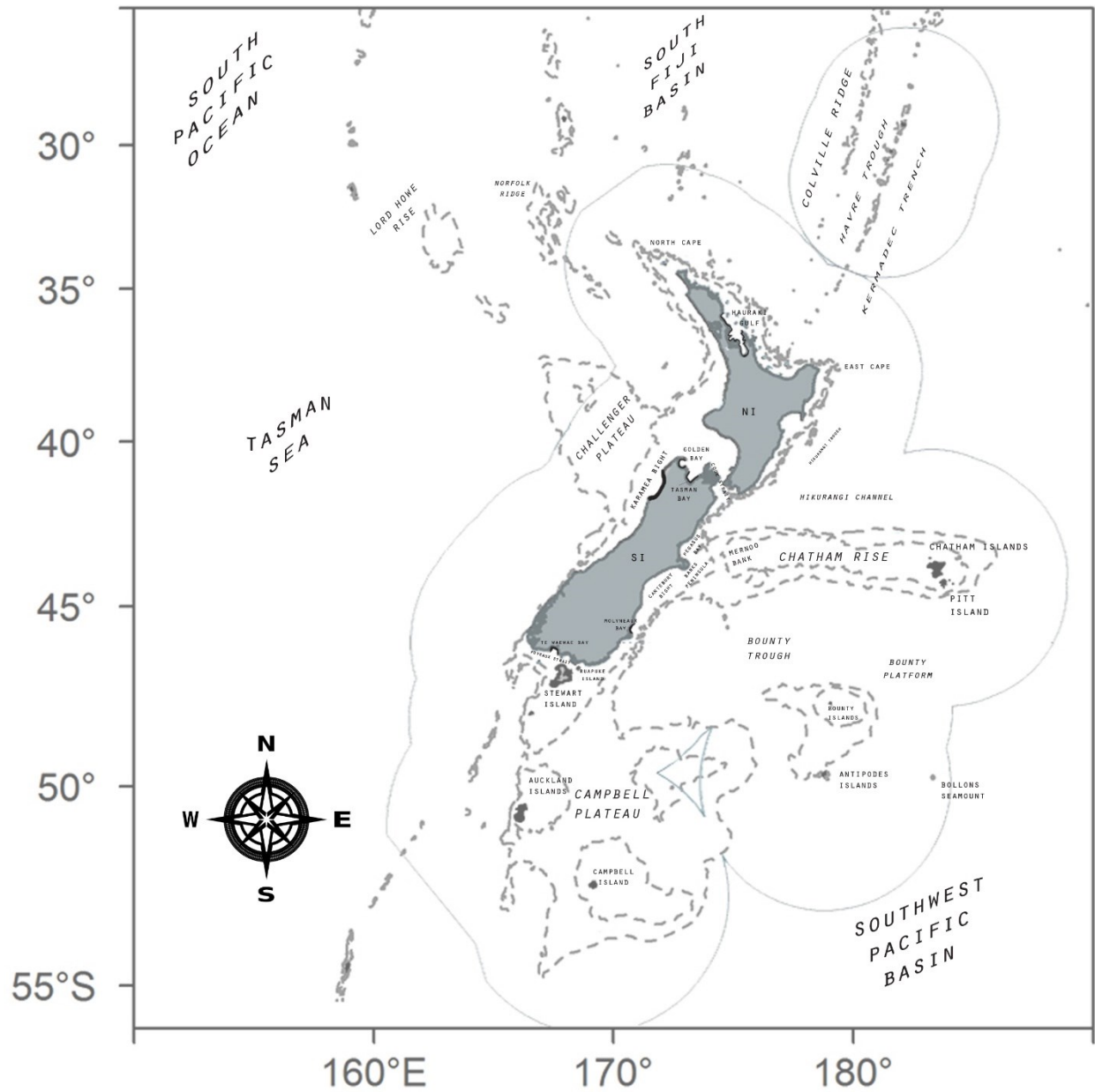
Of the smaller outlying islands, the Bounty Islands are a group of 20 unproductive granite rocks within a small region (a radius of 5 km), and a total land area less than 1.3 km<sup>2</sup>. Campbell Island, the most southerly of the New Zealand subantarctic islands, is approximately 15 km across. The Auckland Islands are the largest subantarctic island group, with a collective area of 625 km<sup>2</sup>. The Snares Islands group are the closest of the subantarctic islands to mainland New Zealand (the North/South islands), lying about 100 km southwest of Stewart Island, the biggest island, located on the south coast of the South island.

The sunken parts of the submerged continental mass known as *Zealandia* form relatively shallow ridges, rises and plateaus seen in the New Zealand EEZ. Major submerged parts are include the Lord Howe Rise, Challenger Plateau, Campbell Plateau, Norfolk Ridge and the Chatham Rise. Consequently, the Challenger Plateau, Chatham Rise and Campbell Plateau support the biggest of New Zealand's fisheries. New Zealand is also known for canyons, seamounts, and trenches because of volcanic activity and tectonic movements (e.g. Kermadec Trench).

### *The New Zealand Exclusive Economic Zone (EEZ) and Water Region Definitions*

The coastal waters of New Zealand extending to the 12 nautical mile limit (territorial waters) will be denoted in this thesis as "coastal waters." The five species described in this thesis are found within the waters of the New Zealand EEZ. An EEZ is a concept ratified at the Third United Nations Conference on the Law of the Sea (1982), where the geopolitical definition excludes waters inside a 12 nautical mile (22 km) limit and extends no more than 200 nautical miles (370 km).

The offshore waters within the EEZ boundary (200 nautical miles) will be referred to as the "New Zealand EEZ." Any depths and/or habitats that are partially included in the EEZ but extend to adjacent areas beyond the 200 nautical mile limit will be discussed as the "New Zealand region."



**Figure 4.** The New Zealand region, showing the boundary line of the Exclusive Economic Zone (EEZ), bathymetry, names of important oceanic features, and major offshore islands.

### 2.1.2 Study Method Approach

The approach utilized in this study will be to use research vessel trawl catches to draw conclusions about habitat use. Several studies have used relative catch rates to infer habitat use (e.g. Michel 2002; Simpfendorfer et al. 2005; Wiley and Simpfendorfer, 2007). An important difference in this thesis research is that the inferences are based on *a priori* expectations drawn from the literature review and not from an unstructured analysis (“data trawling”).

Michel (2002) utilized a relative catch rates approach to study the habitat use of four species of sharks in the Ten Thousand Islands chain between Cape Romano and the mouth of Lostman's River in Florida, U.S.A. Michel (2002) set gillnets in three habitats (gulf edge, transition and backwater) and a preference index showed blacktip sharks (*Carcharhinus limbatus*) preferred the gulf edge habitats, bull sharks (*C. leucas*) preferred backwater habitats and lemon sharks (*Negaprion brevirostris*) avoided the gulf edge habitat. Simpfendorfer et al. (2005) compared catch rates of different sized bull sharks (*C. leucas*) to show that the youngest were found mostly in the riverine area and, as they grew, they moved into coastal lagoons and offshore.

Wiley and Simpfendorfer (2007) also used catch-rate data, using Ivlev's electivity index to examine habitat use patterns of several shark species under three environmental parameters (salinity, temperature and depth) in the Everglades National Park, Florida, U.S.A (Ivlev 1961). Shark sizes varied substantially amongst species, demonstrating the gear was not favorably selective to a specific size of elasmobranchs and all species were caught in all months, indicative of a continuous presence (Michel 2002; Simpfendorfer et al. 2005; Wiley and Simpfendorfer, 2007). Post-hoc comparison of the monthly mean catch rates did not present division amongst the groups, in spite of monthly variations, suggestive of no clear pattern in seasonal abundance (Michel 2002; Simpfendorfer et al. 2005; Wiley and Simpfendorfer, 2007).

Simpfendorfer et al. (2005) recorded *C. leucas* and *N. brevirostris* displaying affinity to depths between 1.2–2.2 m and > 4 m, and avoiding depths < 1.0 m and 2.2 – 3.2 m. *C. limbatus* and *G. cirratum* presented positive relationship, with an increase in electivity with an increase in depth, and *C. limbatus* avoided < 1.5 m, while *G. cirratum* avoided < 2.25 m.

Patterns of habitat use by Chondrichthyes can be crudely assessed via catch-rate data, but present a number of drawbacks. They are unable to provide detailed individual movements that help explain why certain patterns occur (here, biotelemetry methods are needed to assess fine-scale patterns).

Habitat-specific movement can affect catch rates, misidentifying habitat preference. For example, daytime sampling of a species that does DMV might bias the catch rate estimates. Variations in sampling gear can also result in bias catch rates; for example, Heithaus et al. (2007a) demonstrated that the catches of some species were affected by the type of bait used, indicating that catch composition can rely on bait. If a net is used, the mesh size might affect which sizes are caught; also, large animals might out-swim a trawl net. The behavioural strategies that underpin observed distributions of marine species are therefore important to consider. Also important to consider is how the fishing is carried out, as we need to keep fishing methods as constant and comparable as possible. This is why the research trawl database is used, and commercial catch data are not, as the latter are much more susceptible to variability in fishing methods. Fishing isn't done everywhere either, so there are gaps (spatial and temporal) in coverage.

### 2.1.3 Methods

The National Institute of Water and Atmospheric Research (NIWA) presently has the role of Data Manager and Custodian for the fisheries research data owned by the Ministry for Primary Industries (MPI). The *trawl* database (created in 1988) holds data from research trawl surveys, using either dedicated research vessels or chartered commercial fishing vessels (Mackay 2011).

Research trawl data were extracted from *trawl* for the region 160° east – 175° west and 33–55° south. Trawl fishing gear were any bottom or mid-water trawl (gear codes 1-6), and gear performance was ranked at least “satisfactory.” Gear codes obtained were as follows: 1 (bottom trawl), 3 (high operating bottom trawl), 5 (prawn trawl/scampi), and 6 (midwater trawl).

The extracted data set consisted of 618 trawling voyages made by 37 different vessels, over 53 years (1961–2014), and covered a bottom depth range 0 - 2730 m, with only 44 voyages extending deeper than 1500 m. Of these 618 voyages, 109 surveys and 10327 trawls were completed by research ship *RV Tangaroa*, and 52 surveys and 3831 trawls were done by research ship *RV Kaharoa*. For each trawl tow, station details, catch weight by species, and biological sample data, were extracted.

A subset of the research trawl data was made that omitted data prior to 1990, since identification of deep-sea sharks before that point may have been less reliable, and fishing vessels and gears less consistent (M.Dunn, NIWA, pers. comm.). Each tow was assigned a unique code, made up of the trip

code and station number. Trawl start and end coordinates were converted to a decimal format, and all longitudes as degrees east for plotting.

The data fields retained in the analysis dataset were of the unique tow code, trawl start latitude and longitude, minimum and maximum depth, year, month, type of gear (code 1-6), length of tow (n.miles), and bottom and surface temperature. Biological data retained from the catch samples were the MPI species code, percent sampled, and number of fish by length and sex.

Trawl records were then excluded where the percent of species sampled was not applicable (N/A). Where not N/A, the number of fish sampled were scaled by the percent sampled, to give the total number of fish caught in each trip and tow. Records that lacked positional data, and identification of sex, were also omitted. The analysis data subset therefore showed where species were caught and measured and sexed, and did not include fishing events where species were caught and not measured and sexed. Subsets of these data were then taken for each species, and number of fish in each tow divided into four classes: mature males, immature males, mature females, immature females, using literature estimates of length at first maturity (**Table 3**). The number of male, females, immature and mature fish in each tow were then converted to proportions. Relative density for each class was then calculated, as the number caught in that class in that tow divided by the maximum number caught in that class in any tow. The product of relative density and proportions were then plotted on a New Zealand map. Tows of particular interest, due to meeting the criteria for a specific life history habitat area (see below), were checked against other tows made in the same region to establish if this was a persistent occurrence, or if other tows in the same place had different catch compositions and this was more likely to be just chance.

I could not distinguish the following habitat use from our type of dataset, due to no stomach content analysis or reproductive status being available: mating aggregations, food aggregation with possible mating, and exclusive foraging aggregation. In the future, sampling stomach content (prey type, how full the stomach is, prey freshness) and reproductive status (mating scars, hardness of claspers, presence of sperm in spermatid ducts, ripe oocytes) would help to identify these habitat uses and areas.

**Table 3.** Biological characteristics on five species in this thesis: *Callorhynchus milii*, *Hydrolagus novaezealandiae*, *Hydrolagus bemisi*, *Harriotta raleighana*, and *Rhinochimaera pacifica*. L<sub>50</sub>= mean size at first signs of maturity. *c.* refers to chimaera length.

MPI CODE	SCIENTIFIC NAME	LENGTH AT MATURITY	DISTRIBUTION & HABITAT
ELE	<i>Callorhynchus milii</i>	Males L <sub>50</sub> = 50 cm fork length (FL); Females L <sub>50</sub> = 70 cm FL. (Ministry for Primary Industries 2016)	Occurs from East Cape to Stewart Island/Rakiura; most abundant on east coast of South Island (Anderson et al. 1998). <b>Depth range:</b> at least 200m (Anderson et al. 1998).
GSH	<i>Hydrolagus novaezealandiae</i>	Males L <sub>50</sub> = 52 cm; Females L <sub>50</sub> = 62 cm. (Ministry for Primary Industries 2016)	Inhabits the outer continental shelf and upper slope; less common around North Island, Challenger Plateau (Francis et al. 1998). <b>Depth range:</b> 32 m – 800m; most abundant at 150-500 m (Francis et al. 1998).
GSP	<i>Hydrolagus bemisi</i>	Males L <sub>50</sub> = 59 cm; Females L <sub>50</sub> = 69 cm. (Ministry for Primary Industries 2016)	Commonly collected from West Norfolk Ridge to Campbell Plateau (Didier 2002). <b>Depth range:</b> 400-1100 m; commonly found at 600 m. Overlaps with <i>H. novaezealandiae</i> at 400-500 m (Francis et al. 1998; Didier 2002).
LCH	<i>Harriotta raleighana</i>	Unknown; grows up to <i>c.</i> 1.2 m total length (TL). (Goode and Bean, 1895)	Widespread on the slope and a common by-catch of deep water trawling from off Northland to the Campbell Plateau (Kyne and Simpfendorfer 2007). <b>Depth range:</b> 400-2600 m; commonly found at 500-1500 m (Kyne and Simpfendorfer 2007).
RCH	<i>Rhinochimaera pacifica</i>	Unknown; grows up to <i>c.</i> 1.65 m TL. (Mitsukuri 1895)	Worldwide but patchy distribution. Inhabits deep water troughs and plateaus (Mitsukuri 1895). <b>Depth range:</b> 191-1290 m; commonly found at 700 m (Mitsukuri 1895).

## Habitat Criteria

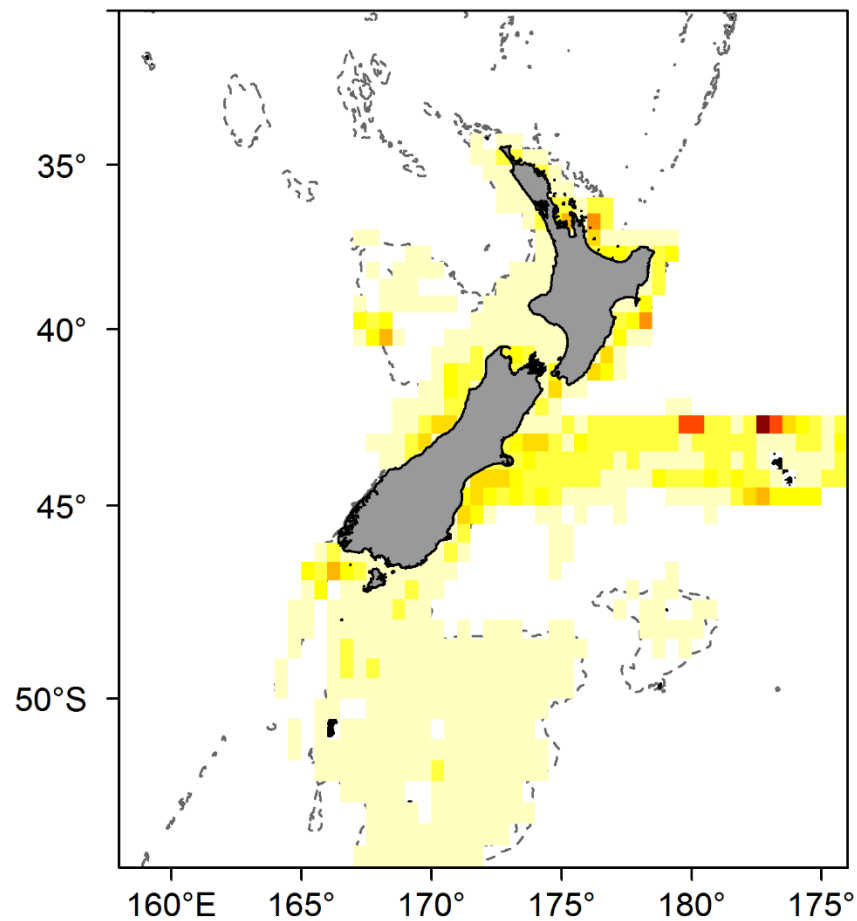
The following *a priori* criteria (**Table 4**) were used to identify catches representing certain habitat uses and are based on composition detailed in **Table 1**. Relative densities were plotted, and tows that met composition criteria were examined in detail.



**Table 4.** Habitat Criteria used to identify catches representing certain habitat uses and based on composition detailed in Table 1.

Habitat	Description
<i>Pupping and Egg-laying Locations</i>	A pupping or egg-laying location consists of a high density of large, sexually mature females, low to nonexistent density of large males ( $<0.25$ ), and some neonates. This is defined as areas/tows where proportion of mature females $> 0.5$ and relative density $> 0.5$ (i.e. product = 0.25).
<i>Nurseries</i>	A nursery (inshore or offshore) location is an area composition of relatively high density of juveniles and a possible low density of adults ( $<0.25$ ). This is defined as areas/tows where proportion of immature males and females $> 0.5$ and relative density $> 0.5$ (i.e. product = 0.25).
<i>Mating Ground</i>	A mating ground comprised of a composition of sexually mature females and males of roughly a 1:1 sex ratio; there can possibly be sub-adults in this area ( $<0.5$ ).
<i>Possible Mating Ground (Lek)</i>	A lek is an area consisting of a high density of mature males and a lower density of mature females. This is defined as areas/tows where proportion of mature males $> 0.5$ and relative density $> 0.5$ (i.e. product = 0.25).
<i>Possible Mating Ground (Aggregation)</i>	A mating aggregation is made up of primarily mature females and males, with some possible sub-adults present ( $<0.5$ ). This is defined as areas/tows where proportion of mature males and females $> 0.5$ and relative density $> 0.5$ (i.e. product = 0.25).
<i>Food Aggregation with Possible Mating</i>	A food aggregation with possible mating is an area consisting of primarily mature females and males, with possible sub-adults present ( $<0.5$ ). This is defined as areas/tows where proportion of mature males and females $> 0.5$ and relative density $> 0.5$ (i.e. product = 0.25).
<i>Exclusive Foraging Ground</i>	An exclusive foraging ground is comprised of mature females and males with possible sub-adults present as well.

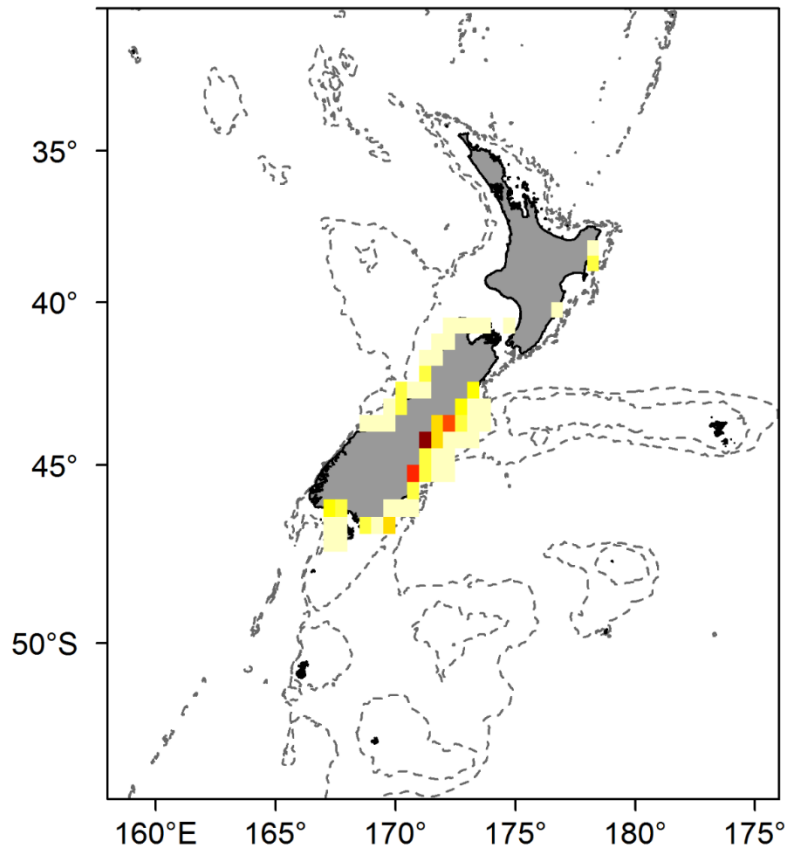
From 1990-2014, a total of 34967 tows were done (**Fig 5**). Regions of particular interest were Hauraki Gulf (snapper surveys), Strawberry Mountain (orange rough spawning), the Graveyard Hills, near the Chatham Islands (orange roughy spawning box), the East Coast South Island Trawl Survey and the edge of the Challenger Plateau (orange roughy spawning).



**Figure 5.** Relative distribution of tows carried out by research survey trawls between 1990-2014. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).

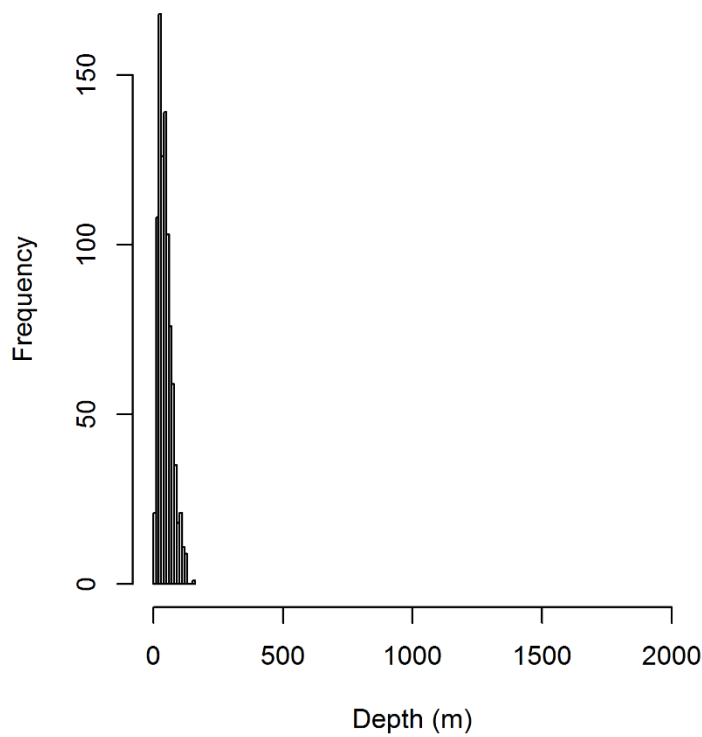
## 2.2 RESULTS

### Elephant Fish (Code: ELE; *Callorhynchus milii*)



**Figure 6.** Relative distribution of number of *Callorhynchus milii* that were caught and measured in research survey trawls between 1990-2014. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).

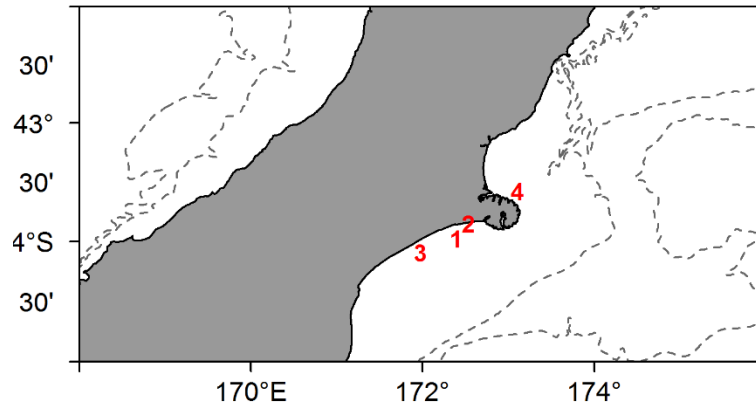
From 1990-2014, there were a total of 895 tows where *Callorhynchus milii* were caught and measured (**Fig 6**). Of these tows, 92.4% of *Callorhynchus milii* were caught using gear code 1. Records of *Callorhynchus milii* were within the coordinates 47.11°S, 37.55°S – 167.4°E, 178.7°E from a minimum depth of 7 meters, maximum depth of 151 meters, and a mean depth of 46.3 meters (**Fig 7**). Relatively high numbers of *Callorhynchus milii* were caught near Invercargill, Nugget Point, and Christchurch.



**Figure 7.** Relative frequency of catch records of *Callorhynchus milii* by depth. Records from research survey trawls (n=895). Depth range of overall dataset (n= 34967) 0-8468 (mean =435.2).

#### *Habitat: Pupping Locations*

Four of the 895 tows satisfied the criteria (given in **Table 5**). The depths of these four tows were all <30 meters, which was shallower than the species average depth of 46.3 meters. These tows were repeated over a number of years in a similar area (**Fig 8, Table 5**).



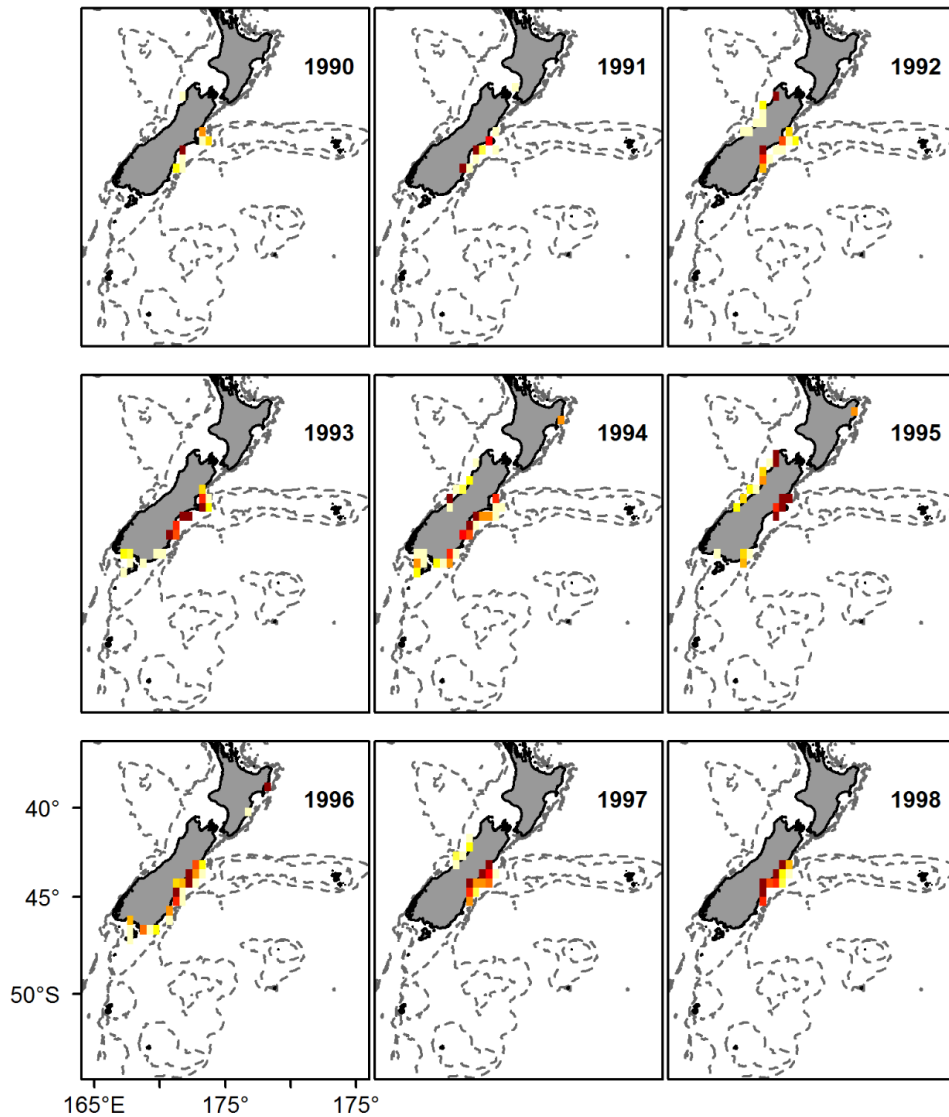
**Figure 8.** The location of the four tows where the criteria were met for pupping locations of *Callorhynchus milii* (see also **Table 5**).

**Table 5.** Details of the four tows where criteria were met for possible pupping location tows of *Callorhynchus milii*. ♀ = females; ♂ = males (see also **Figure 8**).

NO.	DATE	DEPTH (m)	LAT (°S)	LONG (°E)	LARGE ♀	LARGE ♂	SMALL ♂	SMALL ♀
1	Dec 2000	27.5	43.97°	172.39°	202	160	27	53
2	Dec 1999	10.0	43.85°	172.53°	515	66	0	213
3	May 2012	22.5	44.09°	171.97°	235	76	13	172
4	Apr 2012	19.5	43.57°	173.10°	213	3	15	126

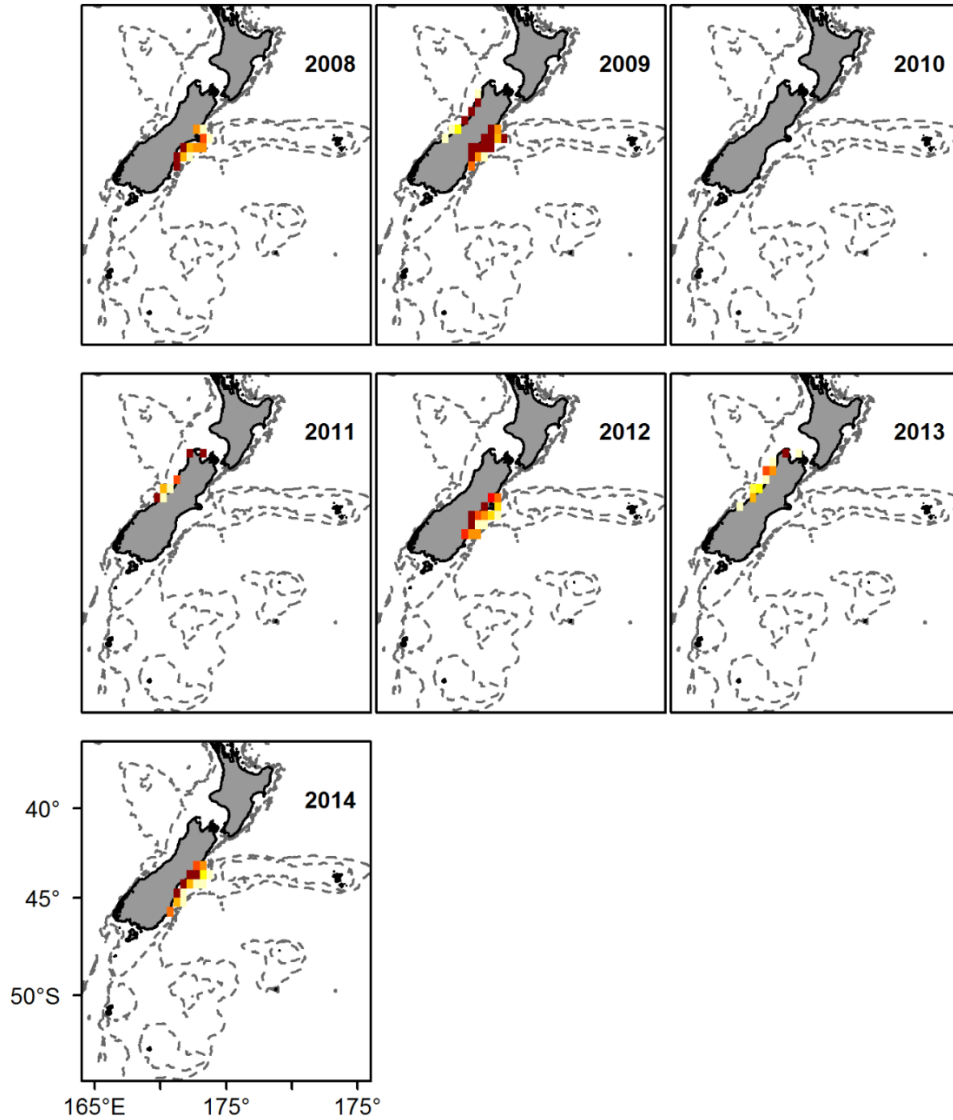
*Juvenile Habitat: Nurseries*

*Callorhynchus milii* distribution found ten tows which met the criteria for nursery grounds off the South Island's eastern coast. Average juvenile depth was 47.74 m with a maximum depth of 129 m and minimum depth of 8 m. Records were between the coordinates 47.08° S, 37.60° S - 167.4° E, 178.6° E (Fig 9).



**Figure 9.** Relative distribution numbers of juvenile *Callorhynchus milii* that were caught and measured in research survey trawls between 1990-1998. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).





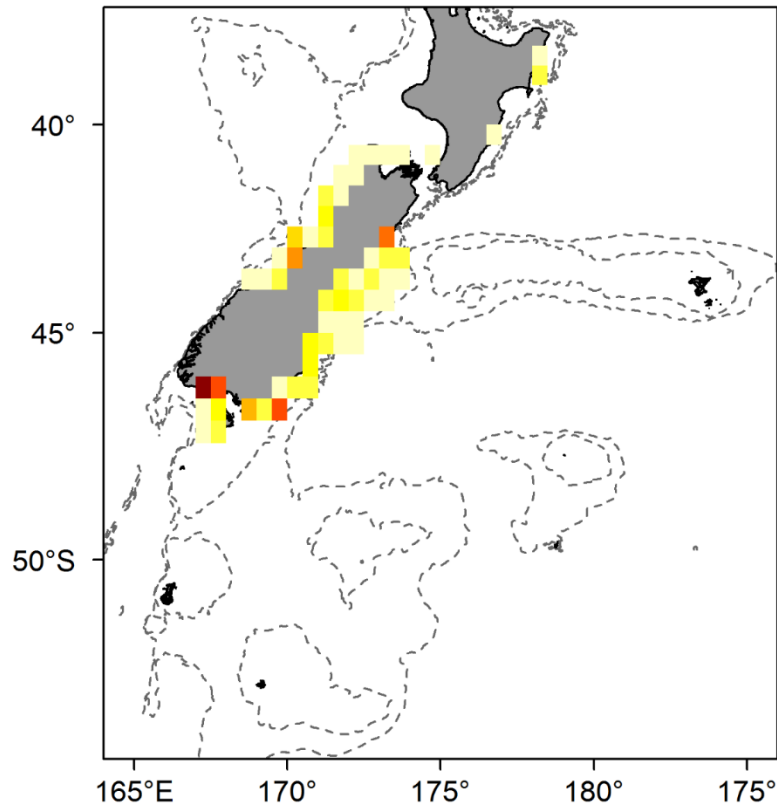
**Figure 9 (cont).** Relative distribution numbers of juvenile *Callorhynchus milii* that were caught and measured in research survey trawls between 2008-2014. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).

Areas meeting the criteria for potential nursery locations from 1990 to 2014 were identified off of the South Island's eastern coast (mostly in Canterbury Bight, Akaroa Harbor, Banks Peninsula around Christchurch), and over multiple years (**Fig 9**). Tows of a particular interest, due to high numbers (over 500) of small females (♀) and males (♂), and low number of large females (typically less than 1% of juvenile total), with virtually no males, are shown in **Table 6**.



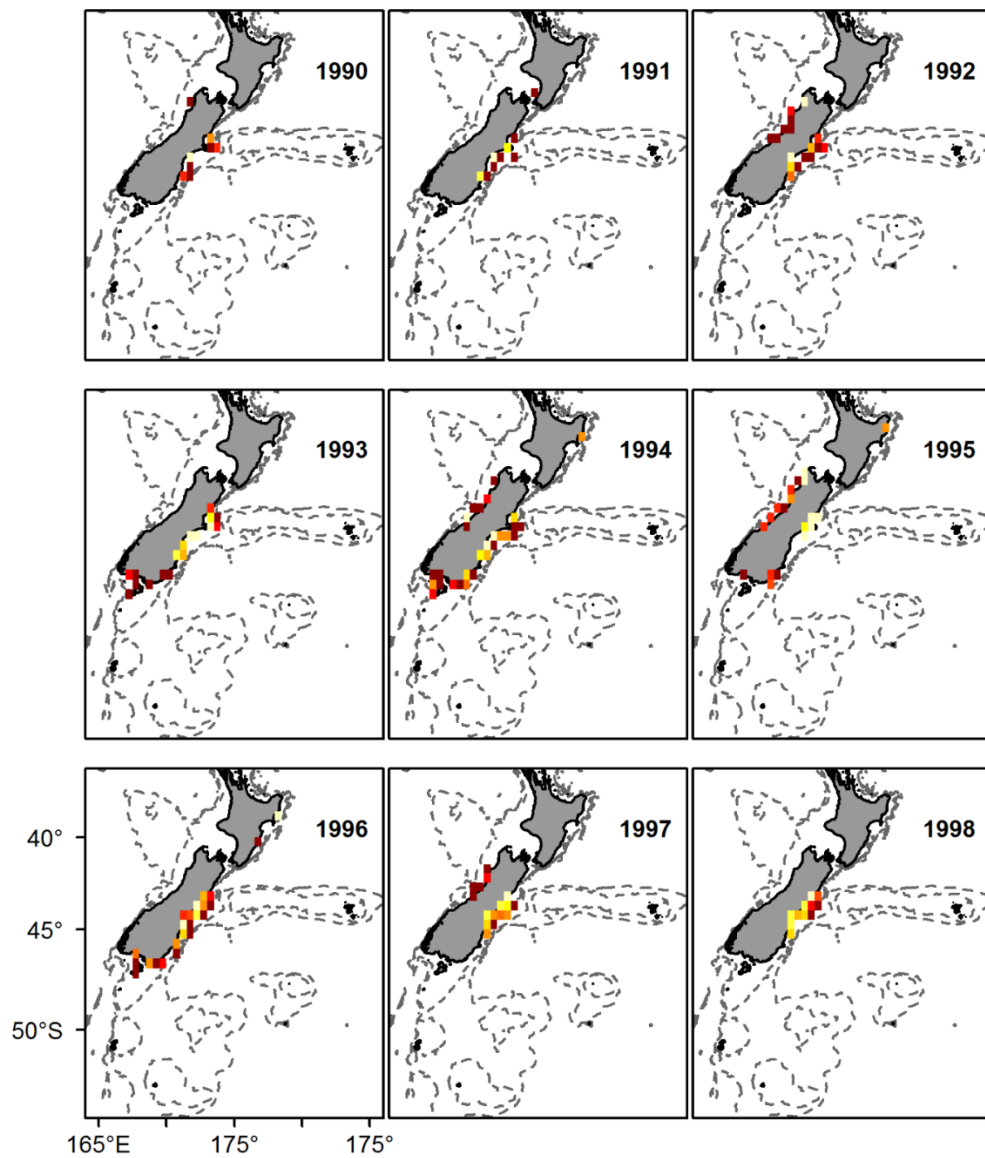
**Table 6.** The details of the tows where criteria were best met for nursery locations for *Callorhynchus milii*. ♀ = females; ♂ = males.

INDEX	DATE	DEPTH (m)	LAT (°S)	LONG (°E)	LARGE ♂	LARGE ♀	SMALL ♀	SMALL ♂
<i>cmp0001_24</i>	Dec 2000	13.5	44.13	171.71	0	13	759	581
<i>cmp0001_28</i>	Dec 2000	19.5	44.19	171.63	0	0	1467	1334
<i>cmp0001_36</i>	Dec 2000	26.5	44.52	171.36	3	1	1226	433
<i>cmp0001_41</i>	Dec 2000	24.5	43.97	172.39	0	0	577	210
<i>cmp9901_15</i>	Dec 1999	27.5	43.98	172.25	1	1	1043	1069
<i>cmp0001_7</i>	Dec 2000	22.5	43.93	172.32	0	24	972	792
<i>kab0705_108</i>	June 2007	28.5	43.97	172.24	0	0	835	540
<i>kab0905_54</i>	May 2009	24.5	44.37	171.46	0	0	495	551
<i>kab1207_81</i>	May 2012	23.5	44.58	171.27	0	0	686	433
<i>kab1207_42</i>	May 2012	20.0	44.35	171.42	0	0	1121	1169

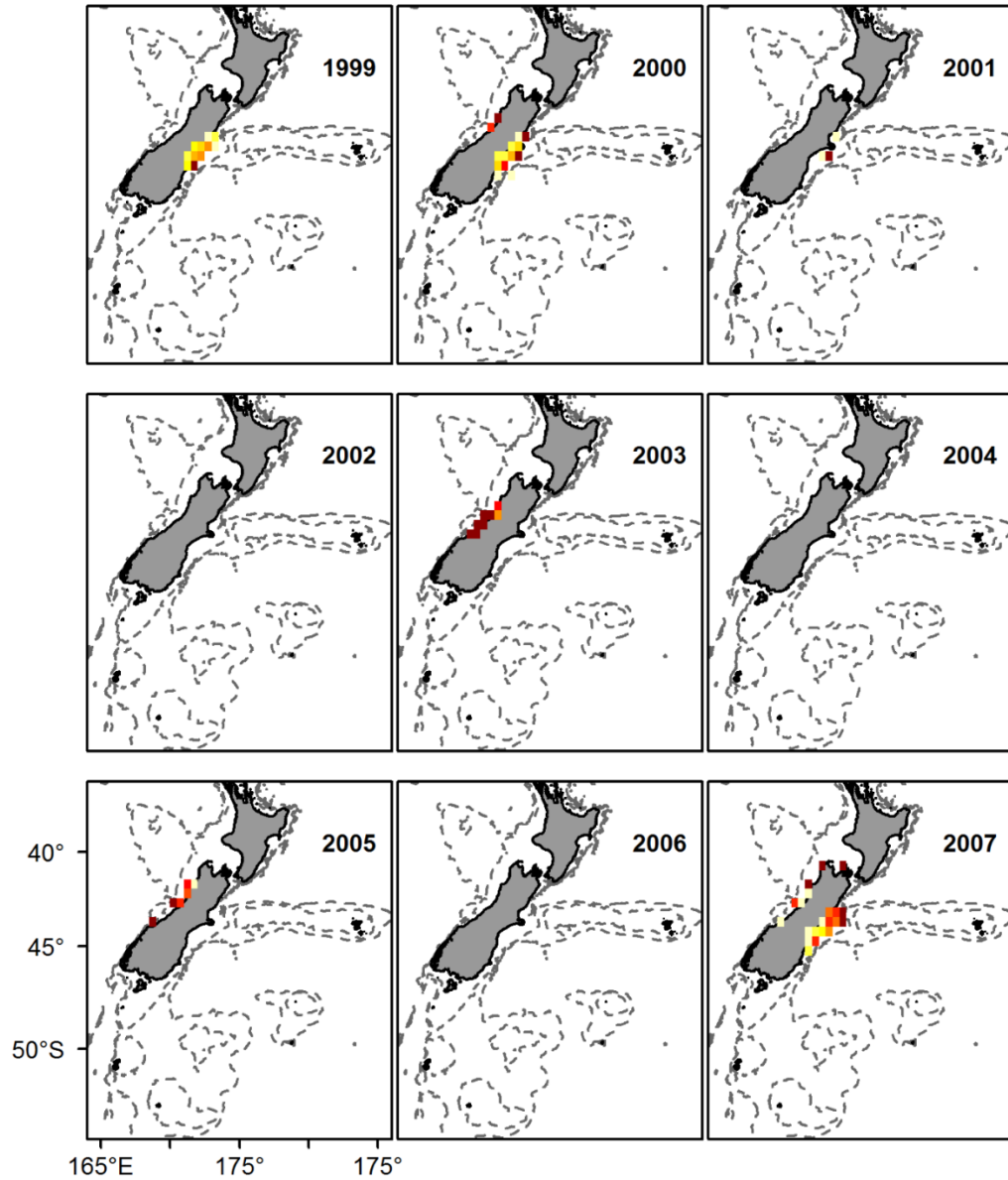


**Figure 10.** Relative distribution numbers of adult *Callorhynchus milii* that were caught and measured in research survey trawls between 1990-2014. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).

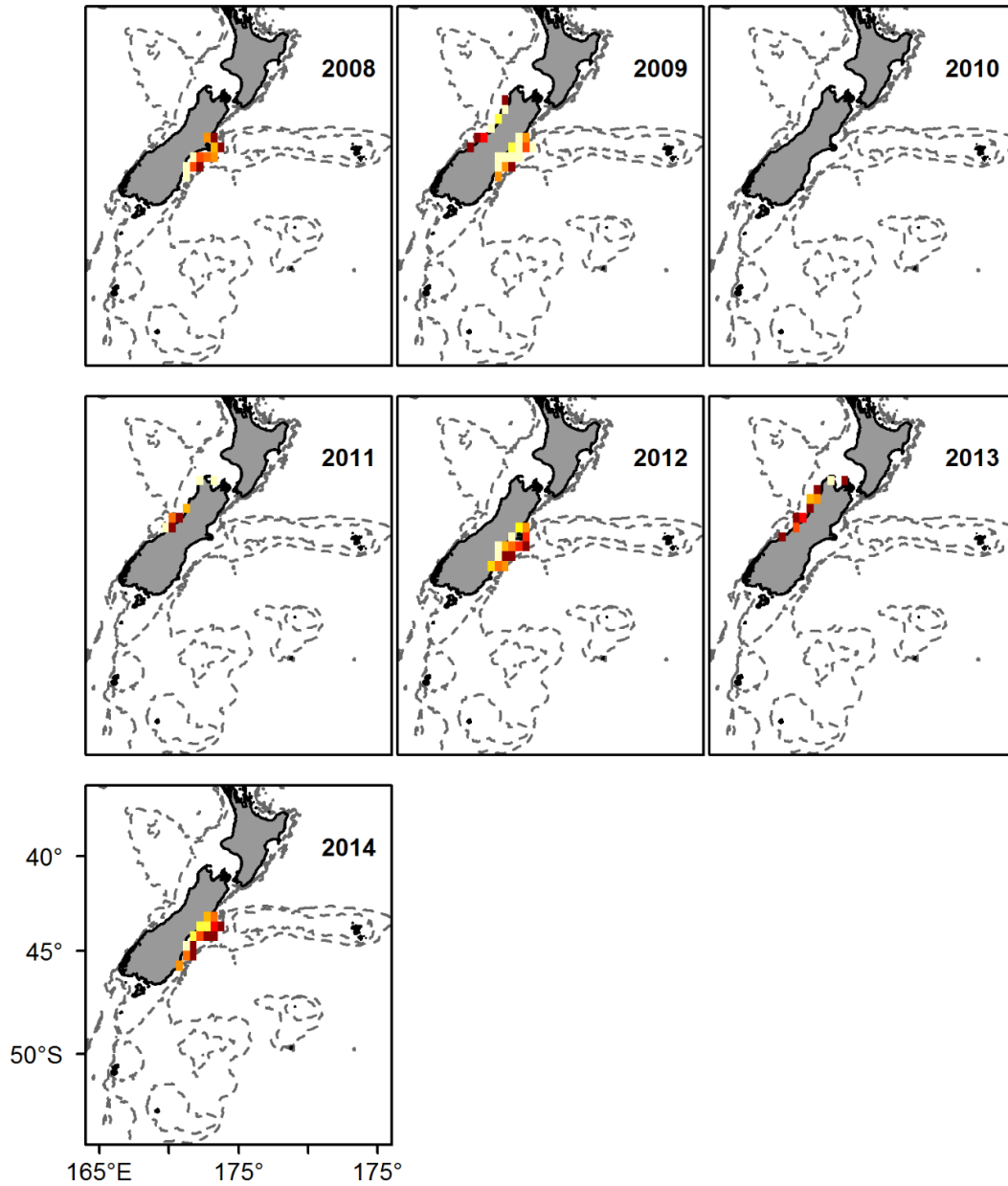
The overall distribution of adults (males and females) of *Callorhynchus milii* between 1990-2014 found high densities between Stewart Island and mainland South Island in Te Waewae Bay, near Invercargill and Christchurch (**Fig 10**). Of these tows, 92.4% of *Callorhynchus milii* were caught using gear code 1. A year by year analysis showed high densities of adults on the South Island west coast as well (**Fig 11**).



**Figure 11.** Relative distribution numbers of adult *Callorhynchus milii* that were caught and measured in research survey trawls between 1990-1998. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).

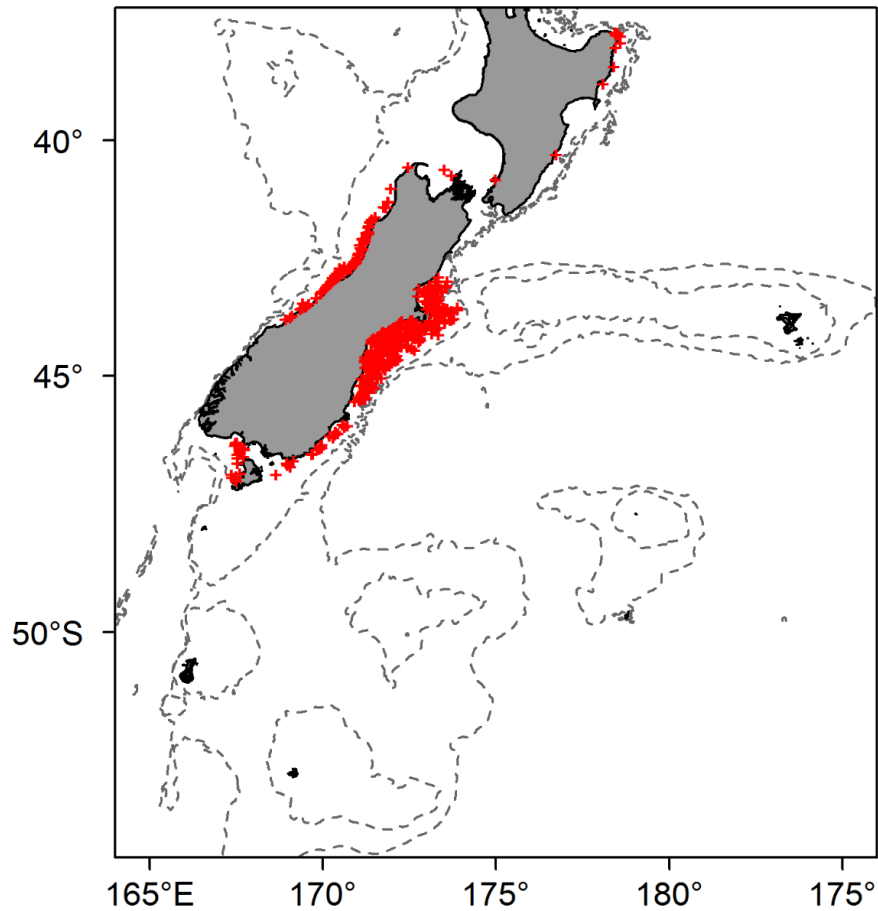


**Figure 11 (cont).** Relative distribution numbers of adult *Callorhynchus milii* that were caught and measured in research survey trawls between 1999-2007. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).



**Figure 11 (cont).** Relative distribution numbers of adult *Callorhynchus milii* that were caught and measured in research survey trawls between 2008-2014. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).

Average adult depth was 48.77 m with a minimum depth of 8 m and maximum depth of 129 m. Adults were recorded between the coordinates 47.11° S, 37.57° S - 167.4° E, 178.6° E.



**Fig 12.** The locations of tows where the criteria were met for mating ground locations of *Callorhynchus milii*. Each “+” delineates an individual tow.

Of the 895 total number of tows, 676 tows met the criteria for a possible mating ground (**Fig 12**). However, most of these tows had <10 individuals caught, and only two tows had high densities that met the criterion for a possible mating ground (**Table 7**). The two tows, which were recorded a year apart in a similar location, had high numbers of individual large females and males, with no juveniles present, and occurred at <30 meters (**Table 7**). These do not meet aggregation criteria (> 0.5 of max).

**Table 7.** Possible mating ground location tows for *Callorhynchus milii*. ♀ = females; ♂ = males.

INDEX	DATE	DEPTH (m)	LAT (°S)	LONG (°E)	LARGE ♀	LARGE ♂
<i>cmp0001_12</i>	Dec 1999	27.5	43.97°	172.39°	202	160
<i>cmp0001_17</i>	Dec 2000	17.5	44.09°	171.89°	22	103

*Adult Habitat: Possible Mating Ground (Lek)*

No tows met the criteria for a lek.

*Adult Habitat: Possible Mating Ground (Aggregation)*

No tows met the criteria for a mating aggregation.

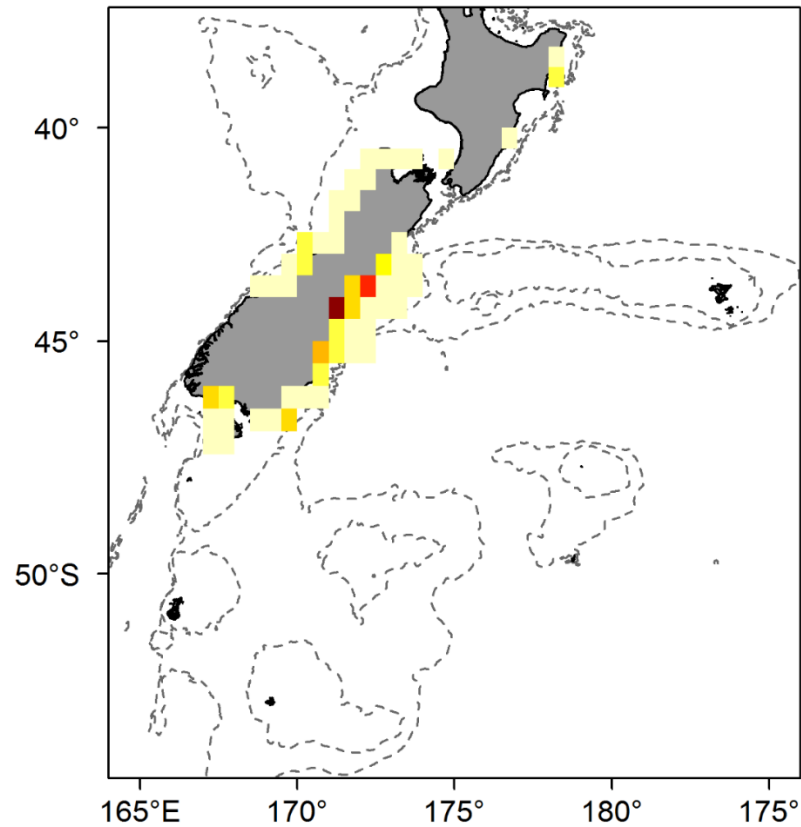
*Adult Habitat: Food Aggregation with Possible Mating*

We could not detect any food aggregation with possible mating (see Methods).

*Adult Habitat: Exclusive Foraging Ground*

We could not detect an exclusive foraging ground (see Methods).

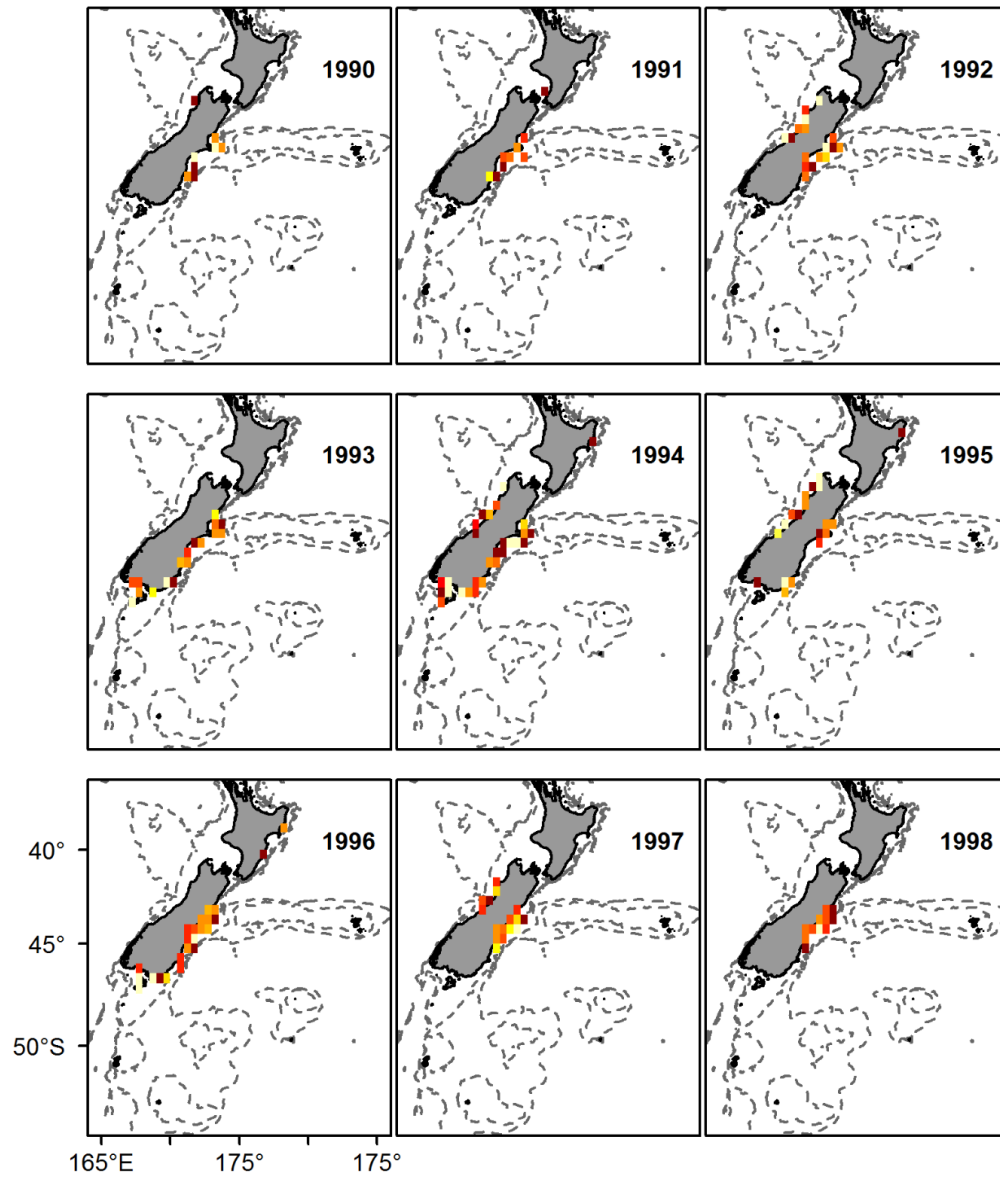
### Female Occurrence



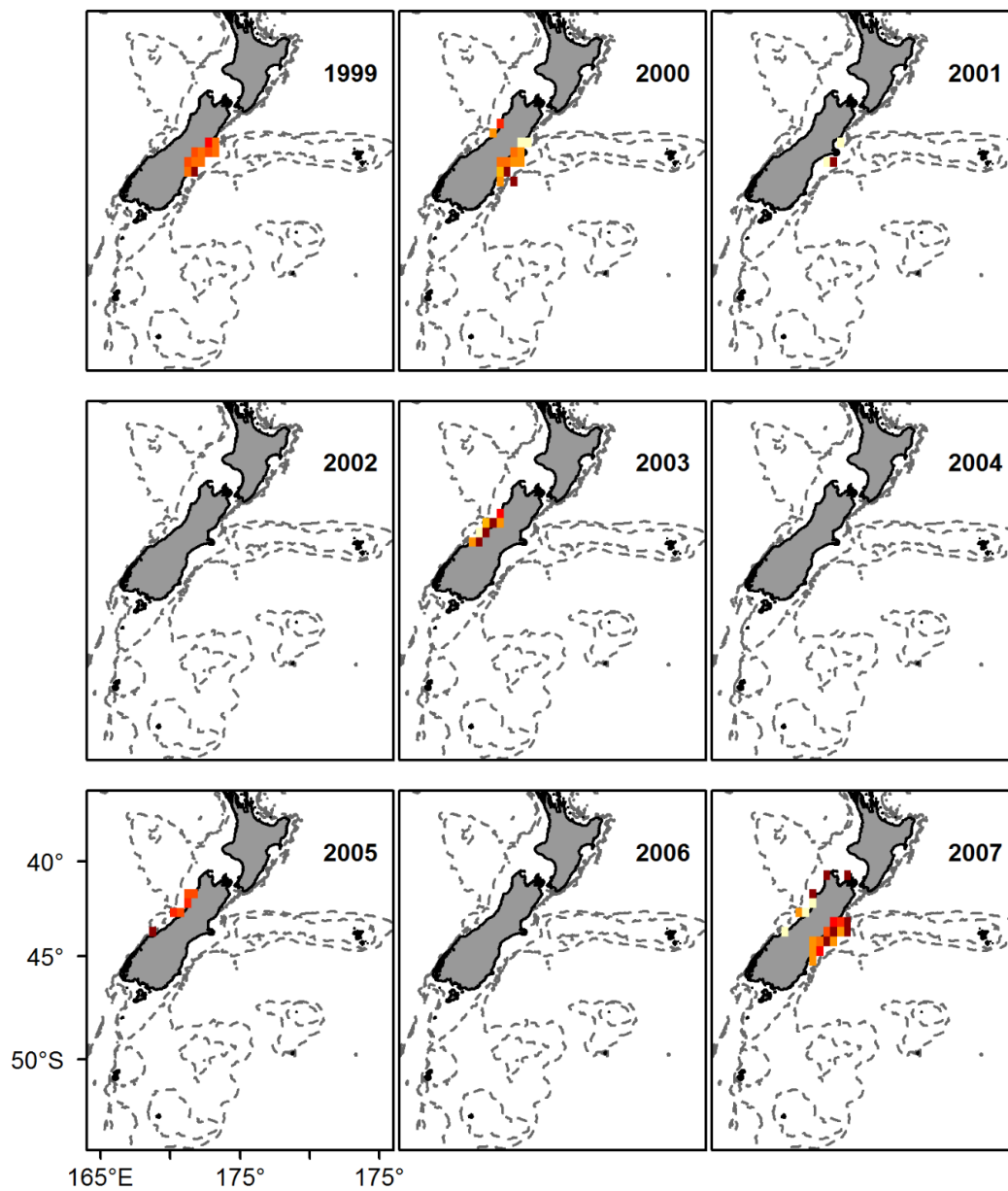
**Figure 13.** Relative distribution of number of female *Callorhynchus milii* that were caught and measured in research survey trawls between 1990-2014. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).

Records of female *Callorhynchus milii* between 1990-2014 found relatively high numbers in Pegasus Bay, Canterbury Bight, Te Waewae Bay and near Poverty Bay (**Fig 13**). Year by year analysis found high numbers of female *C. milii* off South Island's Karamea Bight (year 1990, 1992, 1995, 2007, and 2009), Golden Bay (year 2011, 2013) and Tasman Bay (year 2011, 2013; **Fig 14**). Of 895 tows, 245 tows were female dominated.

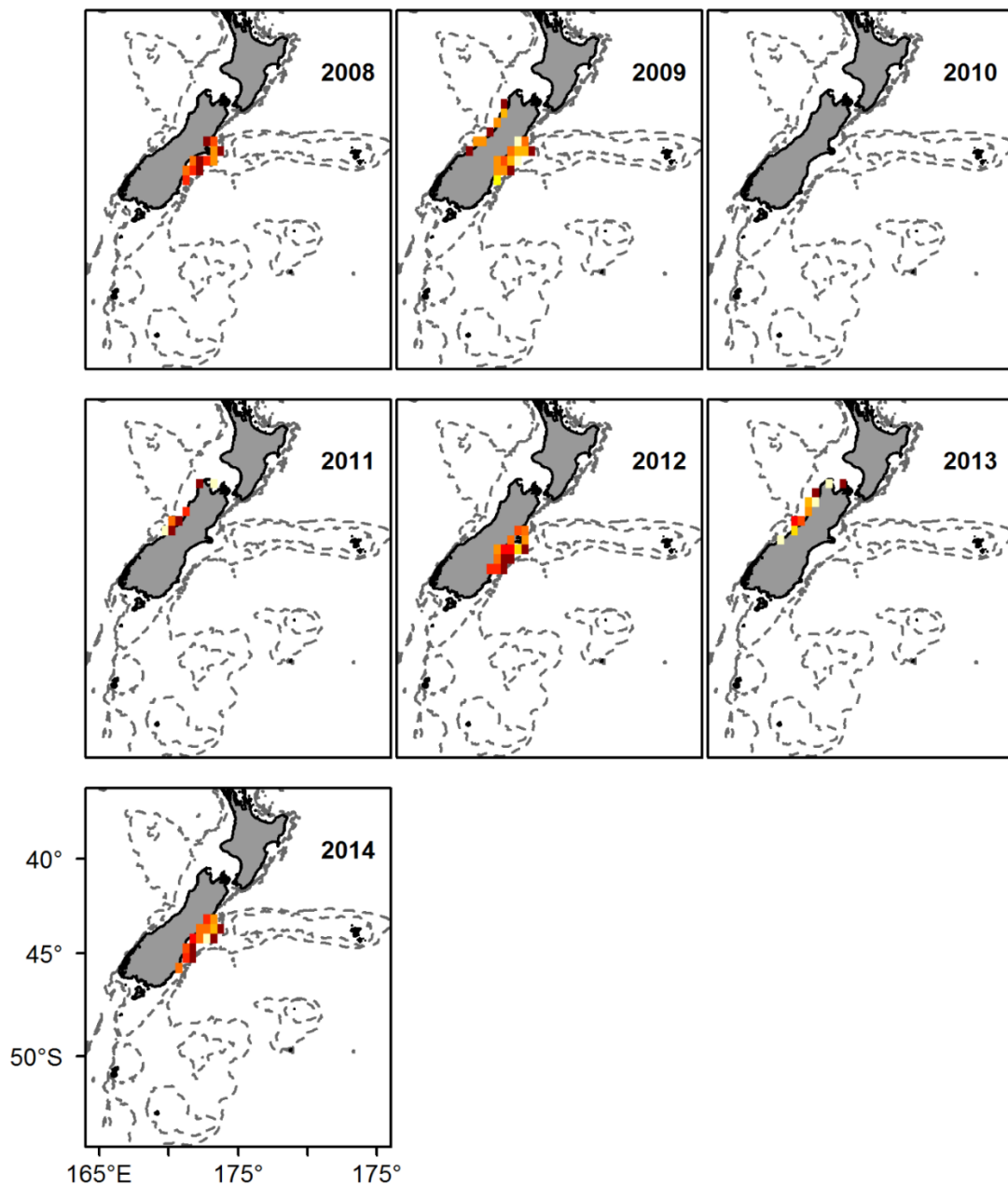




**Figure 14.** Relative distribution numbers of female *Callorhynchus milii* that were caught and measured in research survey trawls between 1990-1998. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).

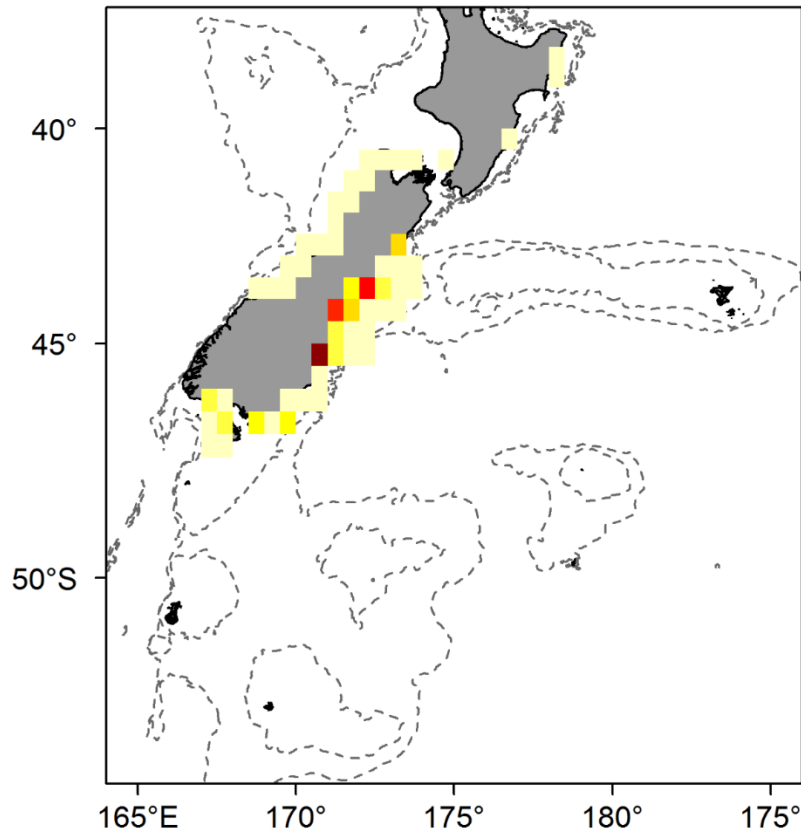


**Figure 14 (cont).** Relative distribution numbers of female *Callorhynchus milii* that were caught and measured in research survey trawls between 1999-2007. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).



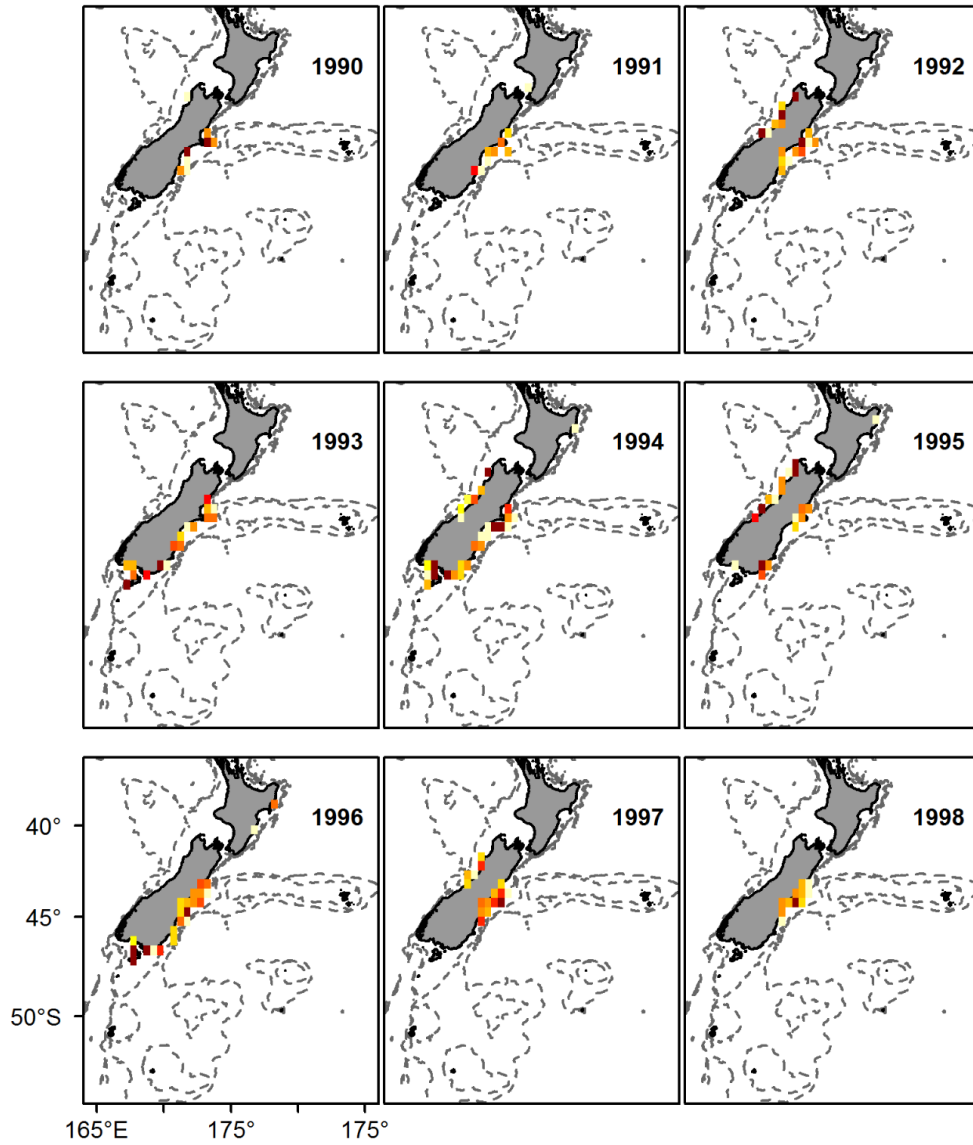
**Figure 14 (cont).** Relative distribution numbers of female *Callorhynchus milii* that were caught and measured in research survey trawls between 2008-2014. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).

### Male Occurrence

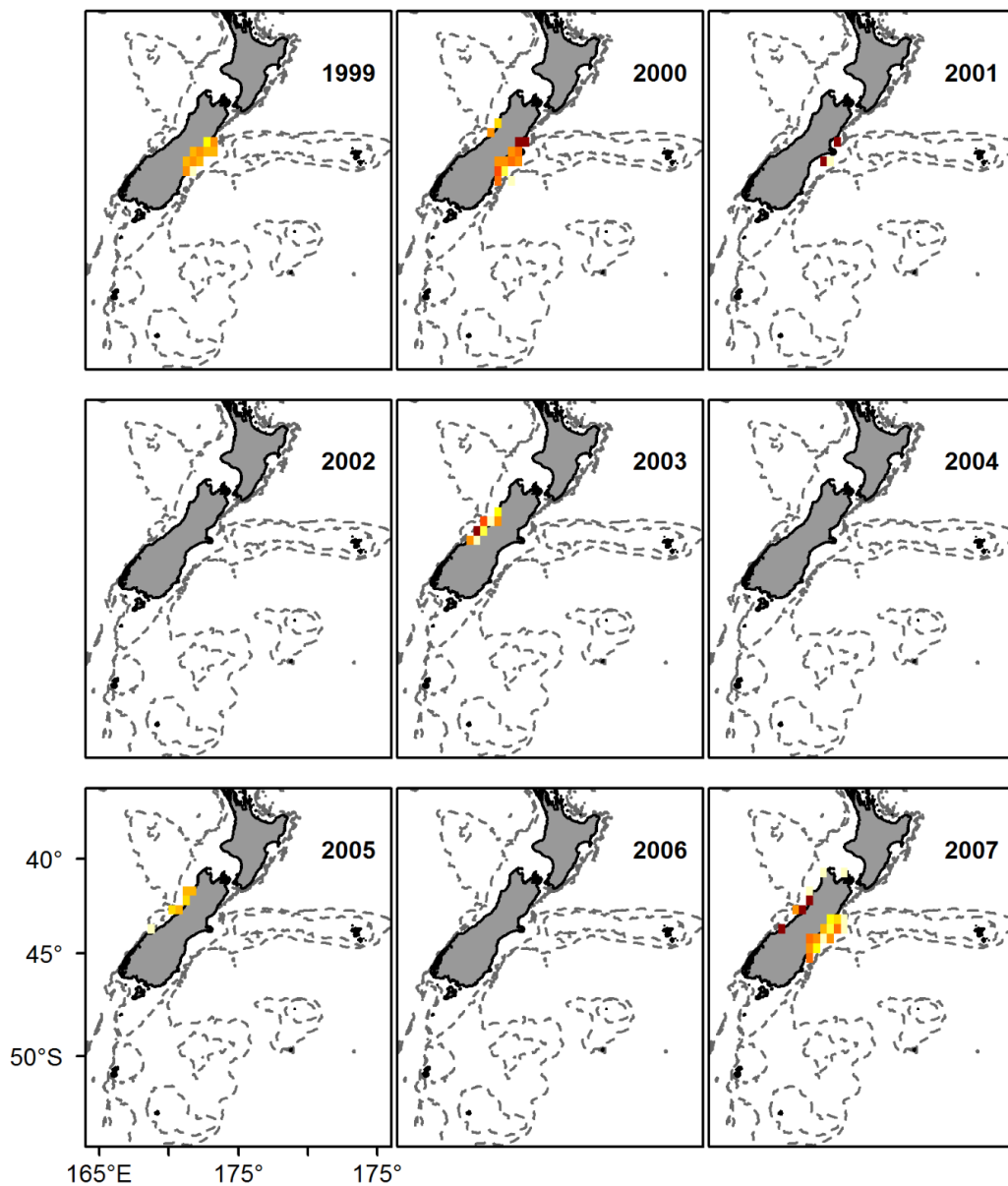


**Figure 15.** Relative distribution of number of male *Callorhynchus milii* that were caught and measured in research survey trawls between 1990-2014. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).

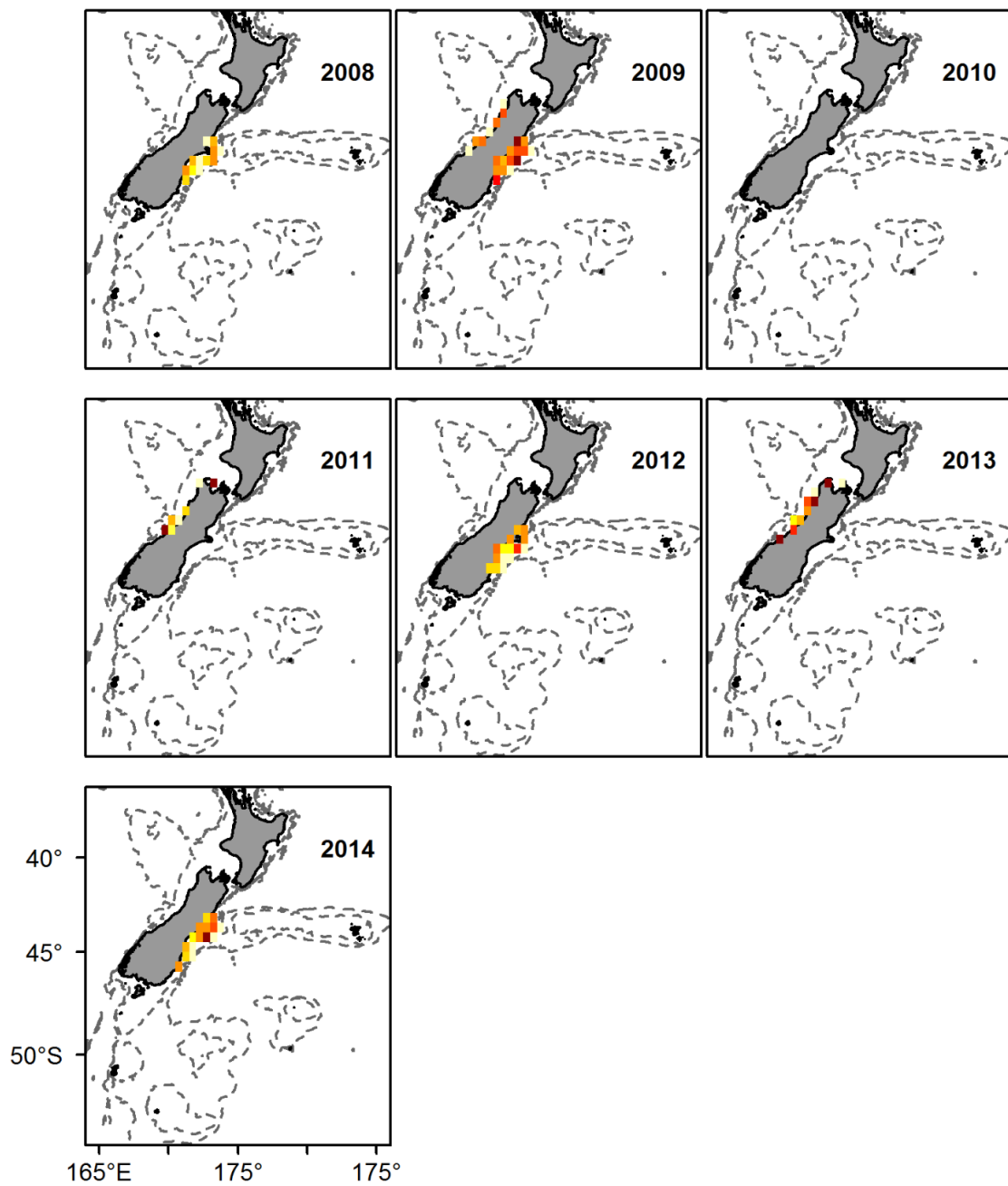
Records of male *Callorhynchus milii* distribution between 1990-2014 found relatively high numbers in Pegasus Bay and Canterbury Bight (**Fig 15**). Year by year analysis found high numbers of male *C. milii* off South Island's western coast (year 1992, 1994, 1995, 1997, 2003, 2007, 2009, 2011, and 2013) and near Stewart Island (year 1993, 1994, 1996, and 2009; **Fig 16**). Of 895 tows, 410 tows were male dominated, but no tows met the criteria of leks.



**Figure 16.** Relative distribution numbers of male *Callorhynchus milii* that were caught and measured in research survey trawls between 1990-1998. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).



**Figure 16 (cont).** Relative distribution numbers of male *Callorhynchus milii* that were caught and measured in research survey trawls between 1999-2007. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).



**Figure 16 (cont).** Relative distribution numbers of male *Callorhynchus milii* that were caught and measured in research survey trawls between 2008-2014. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).

### ***Callorhynchus milii* summary**

From 1990-2014, there was a total of 895 tows that caught and measured *Callorhynchus milii*. Records were within (47.12°S, 37.55°S) and (166.8°E, 178.7°E) (**Fig 6**) with a depth range of 7-151 meters, and an average of 47.28 meters (**Fig 7**).

Of the 895 tows, the following tows were found which matched the criteria for:

1. Pupping grounds (n=4)
2. Nursery grounds (n=10)
3. Mating grounds (n=2)

No tows were found that met the criteria for:

4. Leks

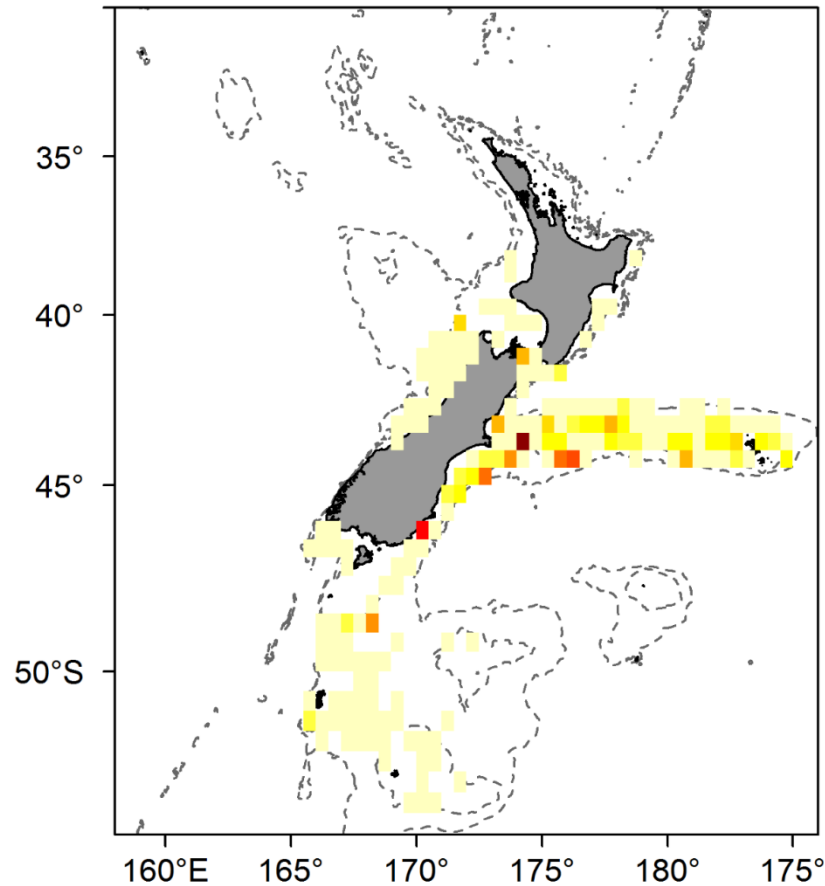
Whilst aggregations occurred, data were not available to distinguish:

5. Food aggregation with possible mating
6. Exclusive foraging grounds

Juveniles and adults tended to be caught inshore of adults (see 2007 in **Fig 9**), and seemed to share similar mean depths. Areas meeting the criteria for potential nursery locations between 1990 to 2014 were identified off of the South Island's eastern coast (notably off Canterbury Bight, Akaroa Harbor, and Banks Peninsula) and over multiple years. Four of the 895 total number of tows may be possible pupping locations, and two tows fell under the criteria for a possible mating grounds, but not mating aggregations. No possible lek-like mating grounds were detected. There were 245 tows that were female-dominated (mature and juvenile) and 410 tows that were male-dominated (mature and juvenile). In 2012 and 2014, two male dominant of interest are persistently in the same location (**Fig 16**).

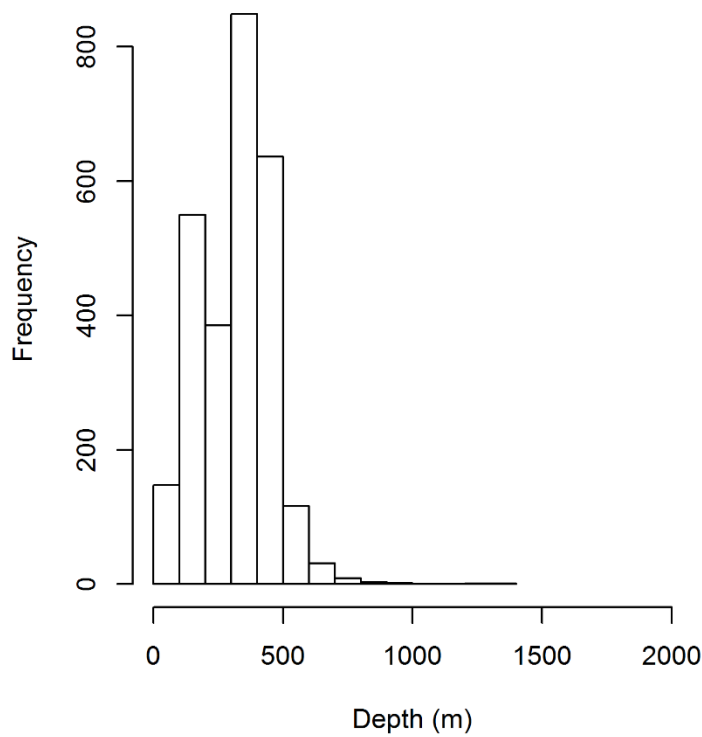


**Ghost Shark (Dark Ghost Shark) (Code: GSH; *Hydrolagus novaezealandiae*)**



**Figure 17.** Relative distribution of number of *Hydrolagus novaezealandiae* that were caught and measured in research survey trawls between 1990-2014. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).

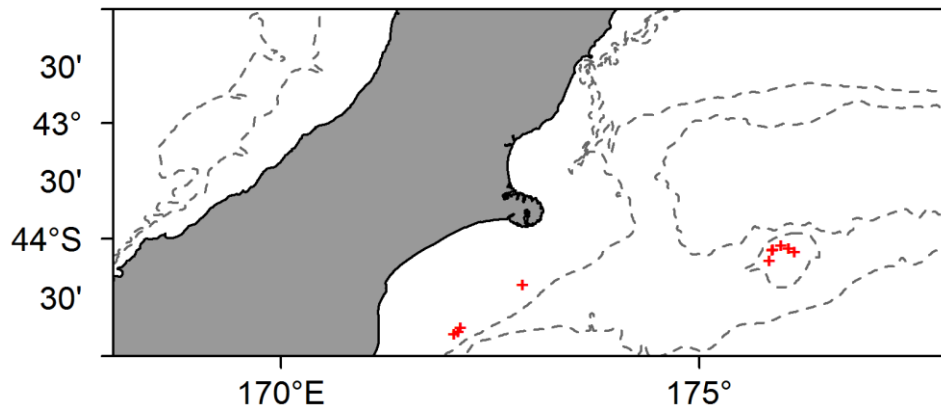
From 1990-2014, there were a total of 2738 tows where *Hydrolagus novaezealandiae* were caught and measured (**Fig 17**). Of these tows, 93.8% of *H. novaezealandiae* were caught using gear code 1; 4% were caught by gear code 2. Records of *H. novaezealandiae* were within the coordinates 53.44°S, 35.06°S – 165.7°E, 184.7°E from a minimum depth of 17 meters, maximum depth of 1399 meters, and a mean depth of 315.4 meters (**Fig 18**). Relatively high numbers of *H. novaezealandiae* were caught near Mernoo Bank, on the Chatham Rise and off Invercargill. No *H. novaezealandiae* were found on the Challenger Plateau or at the north of the North Island.



**Figure 18.** Relative frequency of catch records of *Hydrolagus novaezealandiae* by depth. Records from research survey trawls (n=2738). Depth range of overall dataset (n= 34967) 0-8468 (mean =435.2).

#### *Habitat: Pupping Locations*

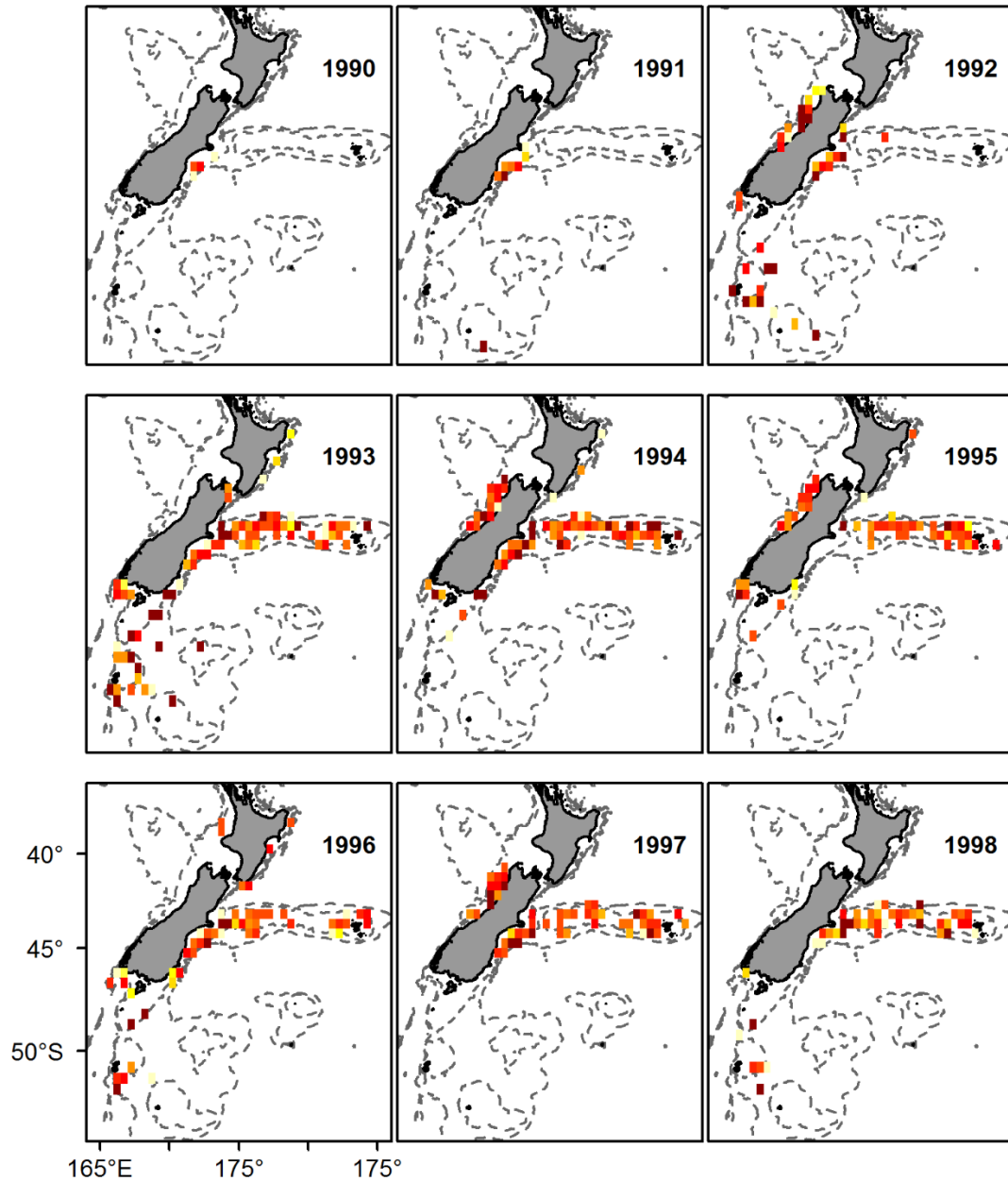
Fourteen of the 2738 tows satisfied the criteria (given in **Table 5**). Of these, nine tows had no large males, high numbers of large females numbers (403 - 810 individuals; **Fig 19**). These tows were repeated over a number of years in a similar area (**Fig 19**).



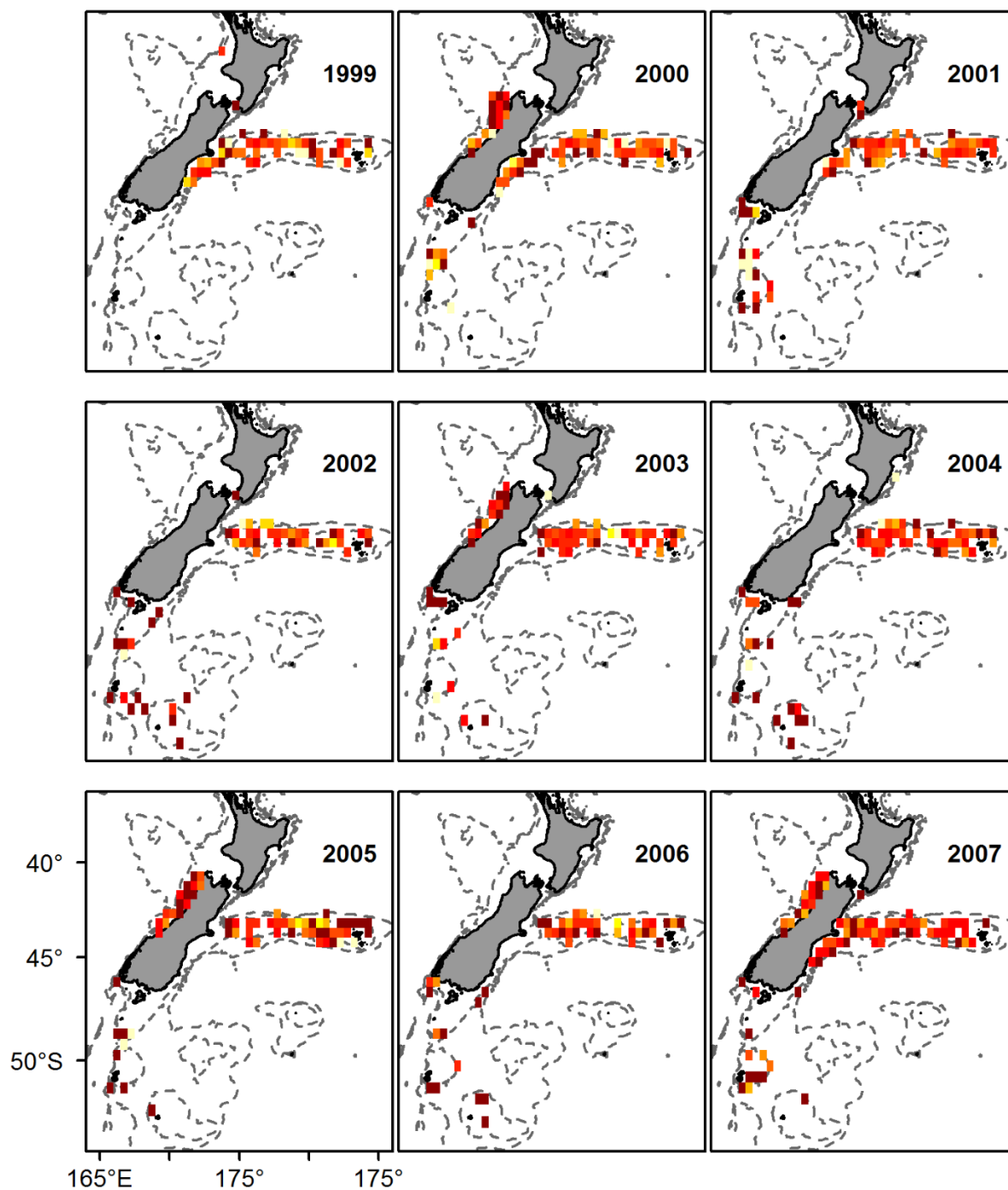
**Fig 19.** The location of the four tows where the criteria were met for pupping locations of *Hydrolagus novaezealandiae*.

#### *Juvenile Habitat: Nurseries*

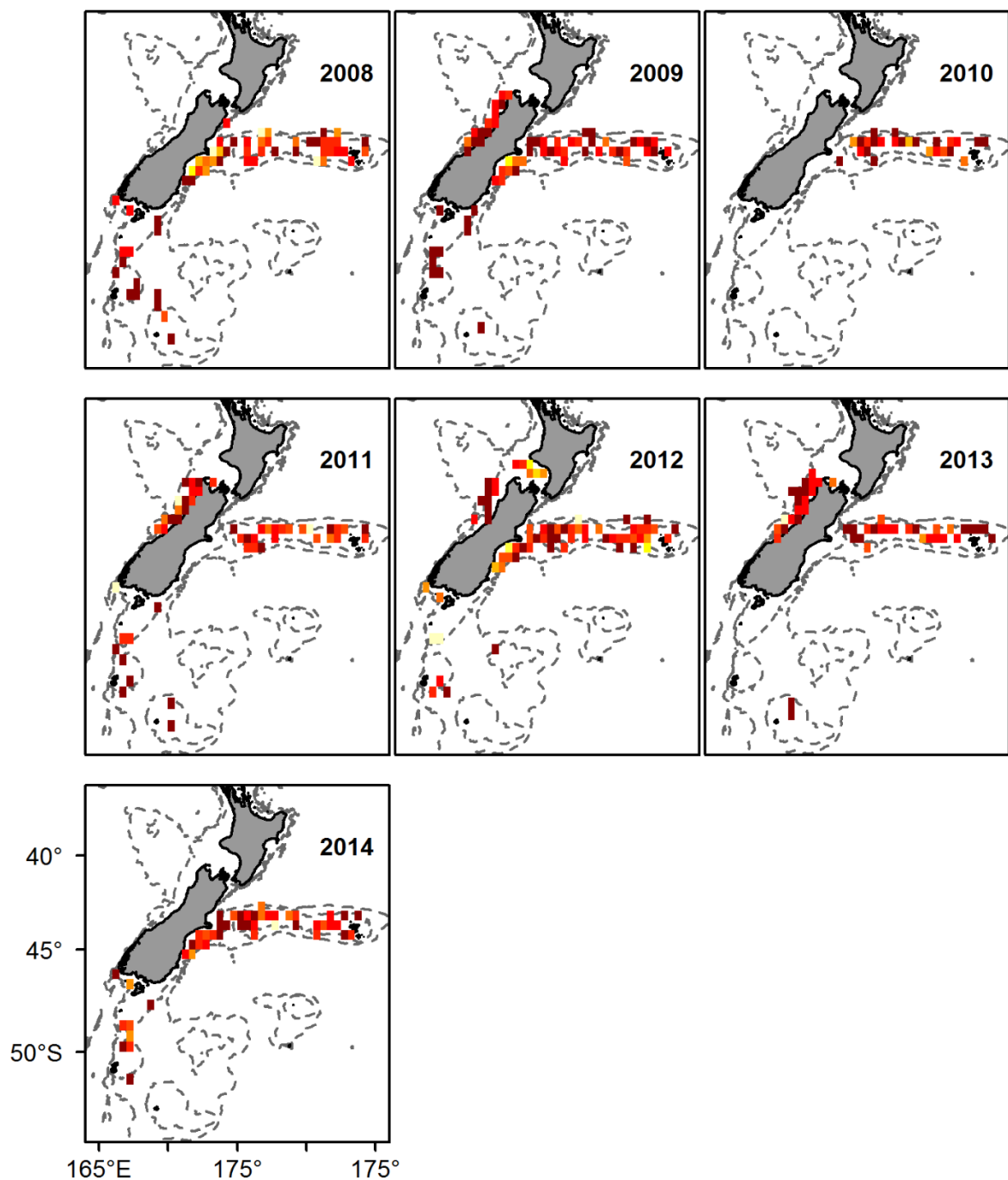
There were no tows which met the criteria for nursery grounds, although there were high densities caught on Chatham Rise (**Fig 20**). Average juvenile depth was 314.6 m with a maximum depth of 412 m and minimum depth of 17 m. Records were between the coordinates 53.44° S, 35.06° S - 165.7° E, 184.7° E.



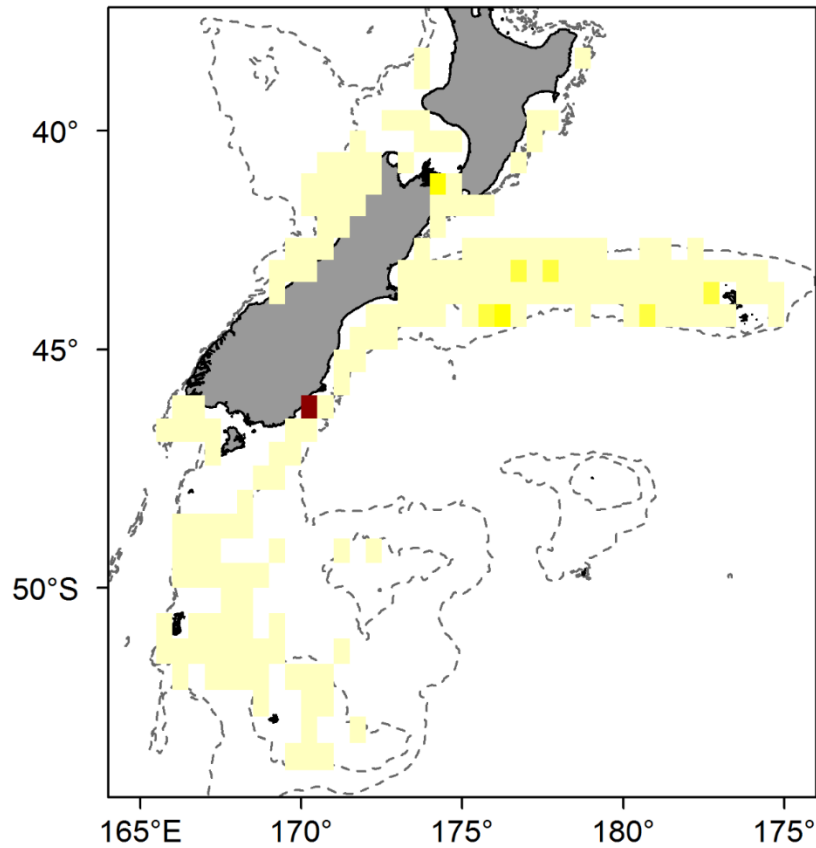
**Figure 20.** Relative distribution numbers of juvenile *Hydrolagus novaezealandiae* that were caught and measured in research survey trawls between 1990-1998. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).



**Figure 20 (cont).** Relative distribution numbers of juvenile *Hydrolagus novaezealandiae* that were caught and measured in research survey trawls between 1999-2007. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).

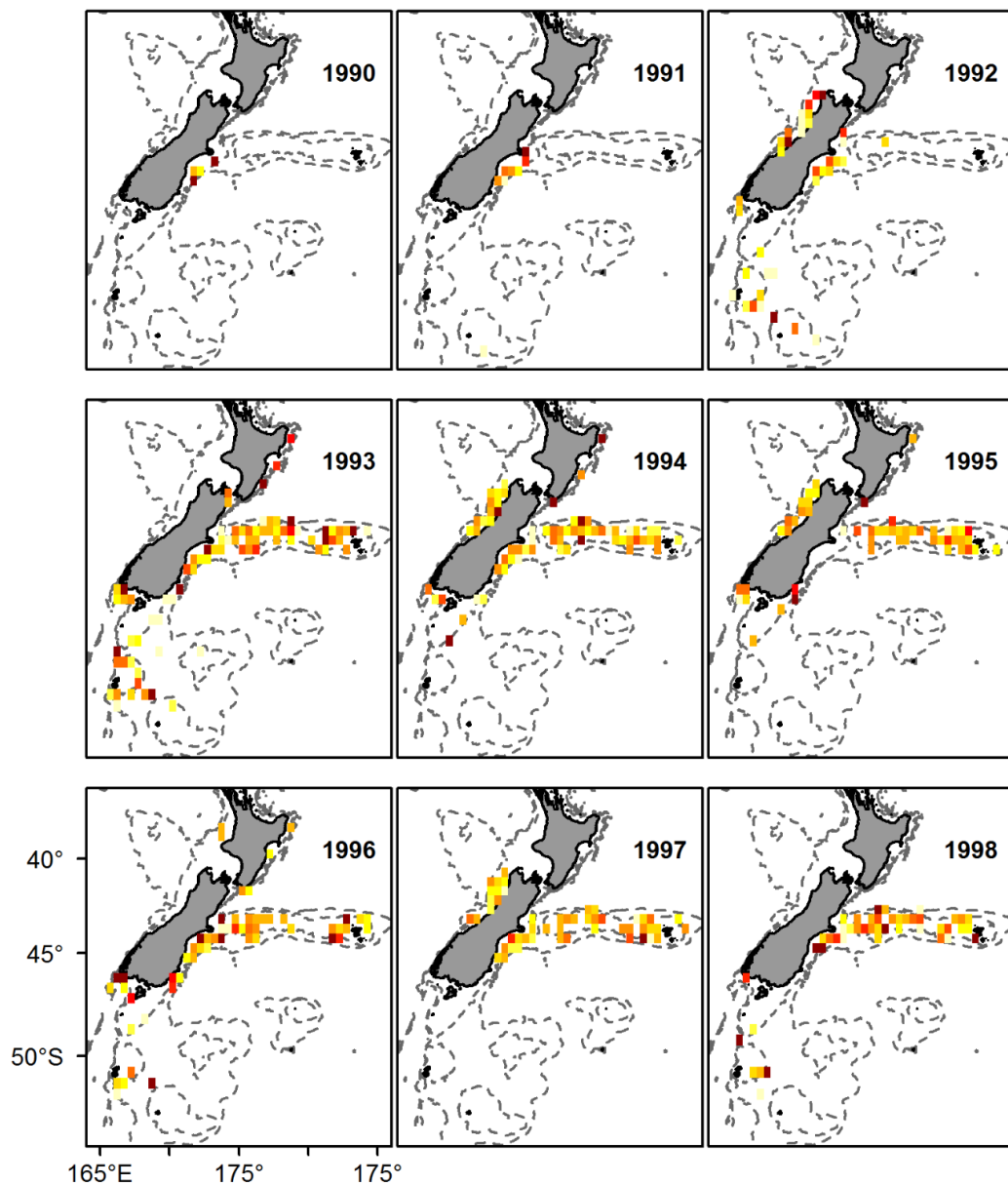


**Figure 20 (cont).** Relative distribution numbers of juvenile *Hydrolagus novaezealandiae* that were caught and measured in research survey trawls between 2008-2014. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).



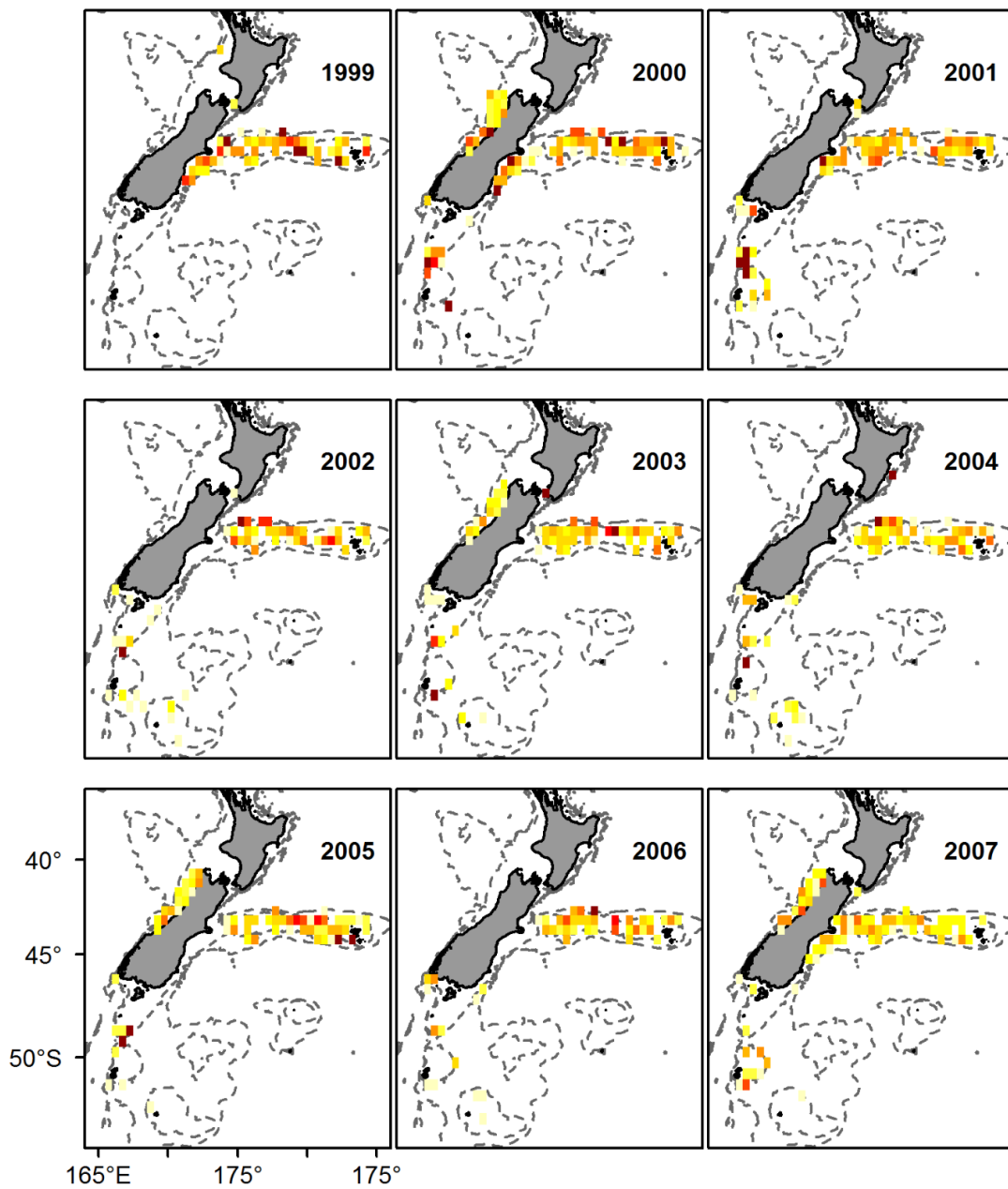
**Figure 21.** Relative distribution numbers of adult *Hydrolagus novaezealandiae* that were caught and measured in research survey trawls between 1990-2014. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).

The overall distribution of adults (males and females) of *Hydrolagus novaezealandiae* between 1990-2014 found high densities near Invercargill (**Fig 21**). Year by year analysis found high numbers of adults between mainland South Island and Stewart Island (year 1993, 1994, 1996, 2001, 2012, 2014) and South Island's Christchurch (**Fig 22**).

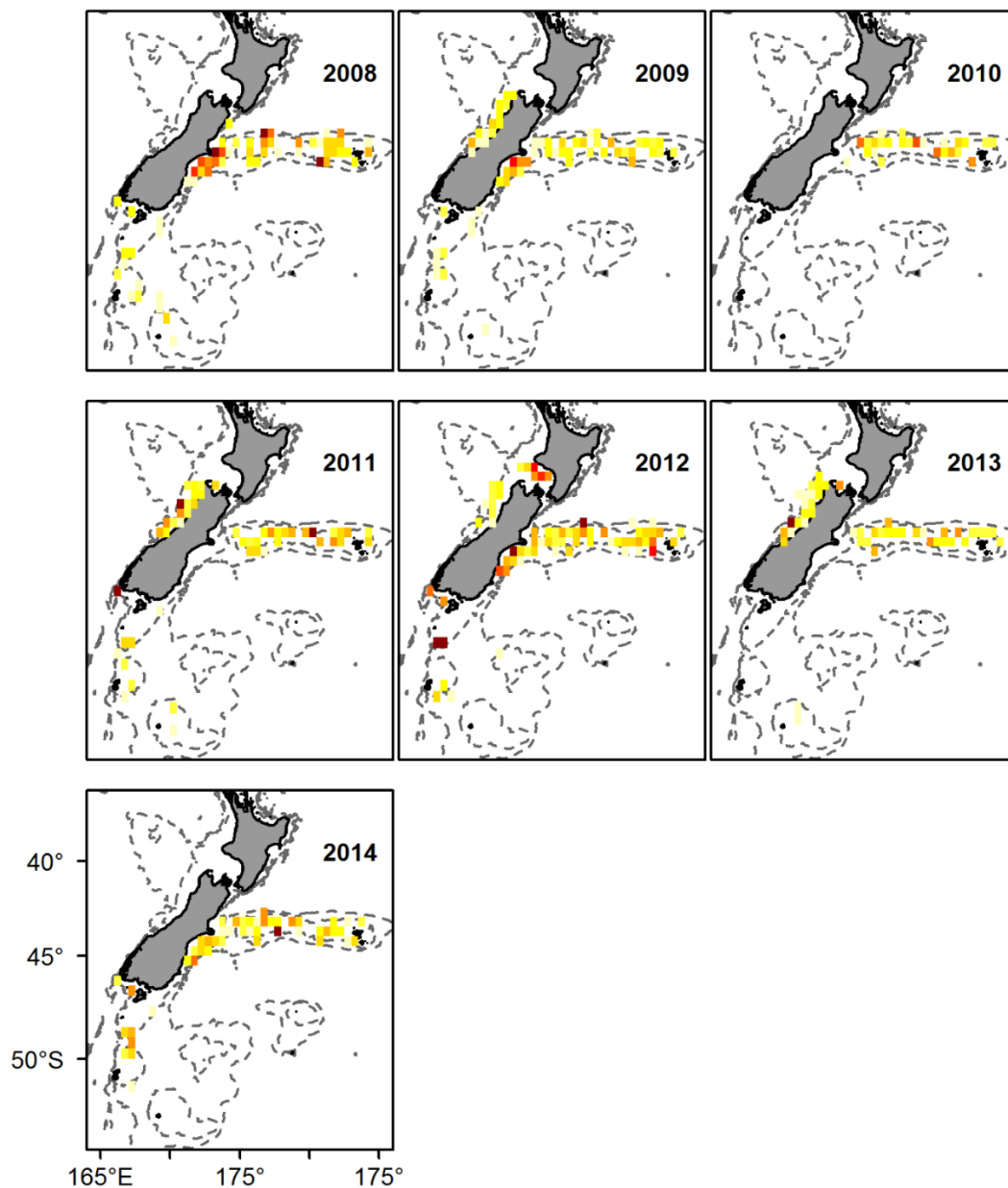


**Figure 22.** Relative distribution numbers of adult *Hydrolagus novaezealandiae* that were caught and measured in research survey trawls between 1990-1998. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).





**Figure 22 (cont).** Relative distribution numbers of adult *Hydrolagus novaezealandiae* that were caught and measured in research survey trawls between 1999-2007. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).



**Figure 22 (cont).** Relative distribution numbers of adult *Hydrolagus novaezealandiae* that were caught and measured in research survey trawls between 2008-2014. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).

Average adult depth was 298.4 m with a minimum depth of 34 m and maximum depth of 750.5 m. Adults were recorded between the coordinates 52.37° S, 35.55° S - 165.7° E, 184.7° E.

#### *Adult habitat: Mating Ground*

Of the 2738 total number of tows, 195 tows met the criteria for a possible mating ground. However, all of these tows had low single-digit individuals of each sex, except one tow, *kab9204\_22* (41.29° S, 171.03° E), at 191 meters deep recorded 12 large males with nine large females. This tow was done in March 1992, and is not replicated in subsequent years.

#### *Adult Habitat: Possible Mating Ground (Lek)*

Of the 2738 total number of tows, 45 tows met the criteria for a possible lek. A closer look at the data revealed only one tow of interest, *kab1207\_13*, at 43.03° S, 173.60° E. Carried out on 29 April 2012, it retrieved 41 large males, 13 large females, 26 small males and 4 small females. Nine tows were done between April and May in similar latitudes ( $\pm 0.05^\circ$ ) between 1972 and 2012, with only that Kaharoa research vessel (station no. 13) matching a lek-like criteria.

#### *Adult Habitat: Possible Mating Ground (Aggregation)*

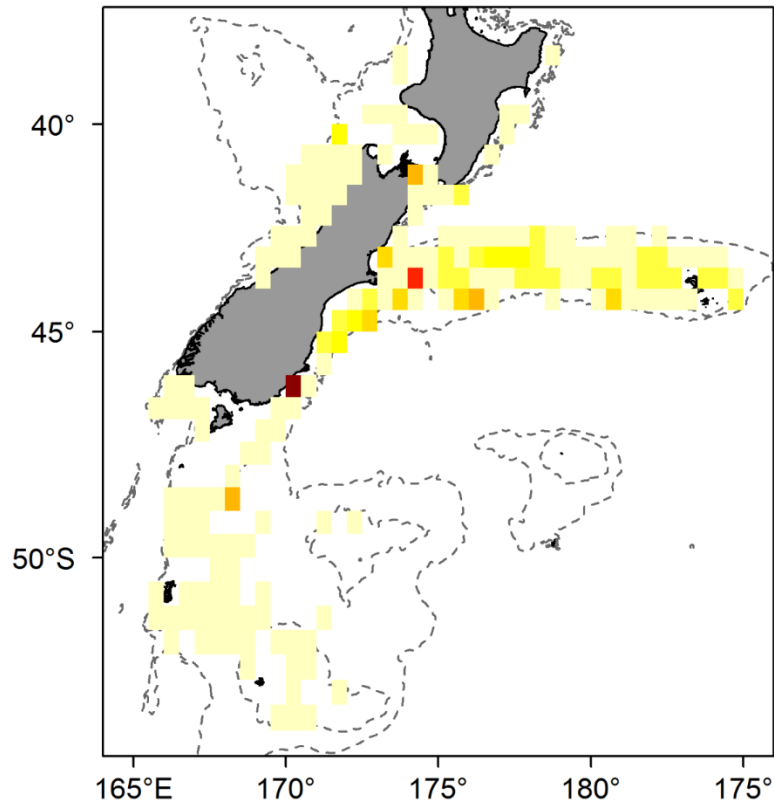
No tows met the criteria for a mating aggregation.

#### *Adult Habitat: Food Aggregation with Possible Mating*

We could not detect any food aggregation with possible mating (see Methods).

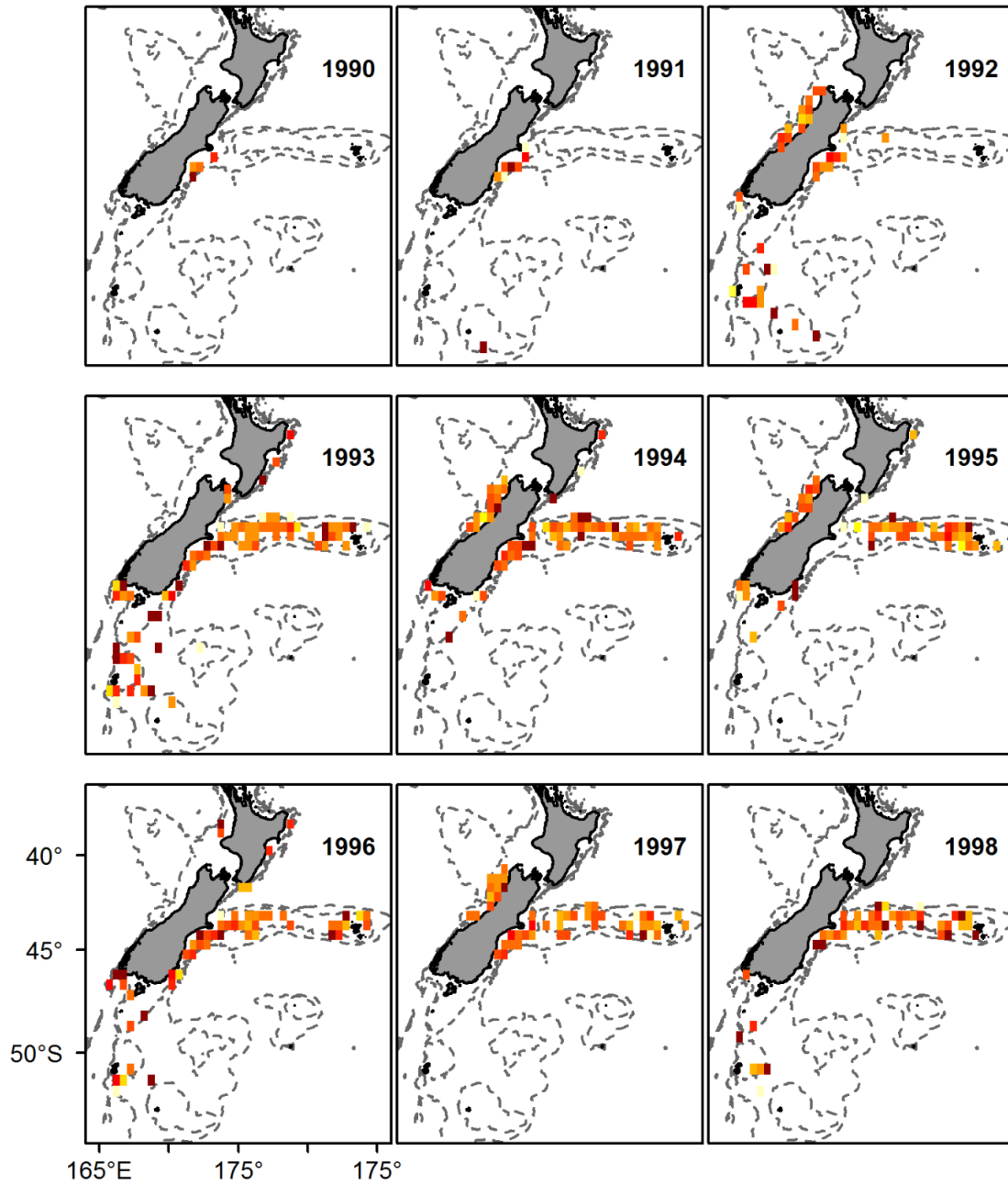
#### *Adult Habitat: Exclusive Foraging Ground*

We could not detect an exclusive foraging ground (see Methods).

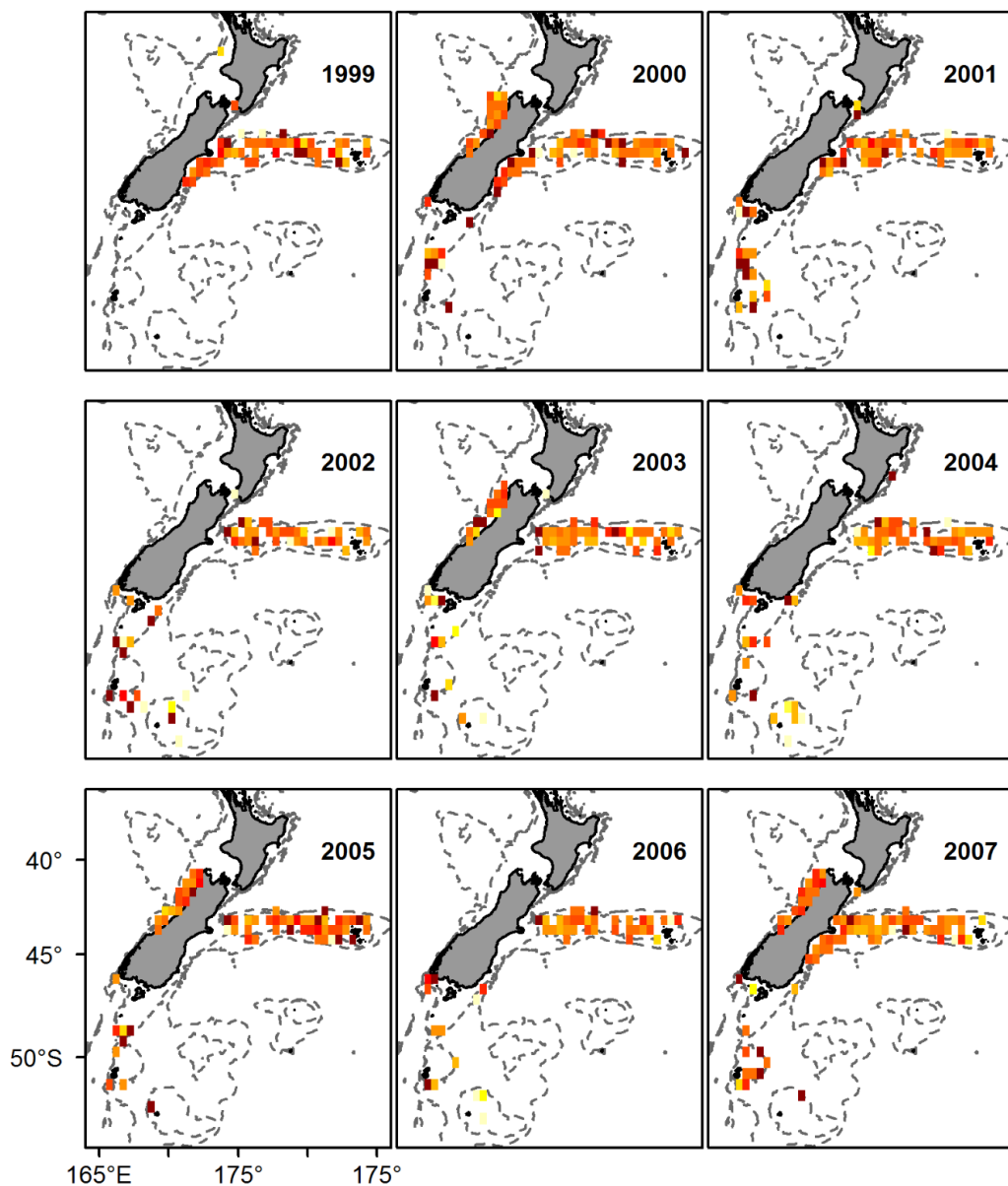


**Figure 23.** Relative distribution of number of female *Hydrolagus novaezealandiae* that were caught and measured in research survey trawls between 1990-2014. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).

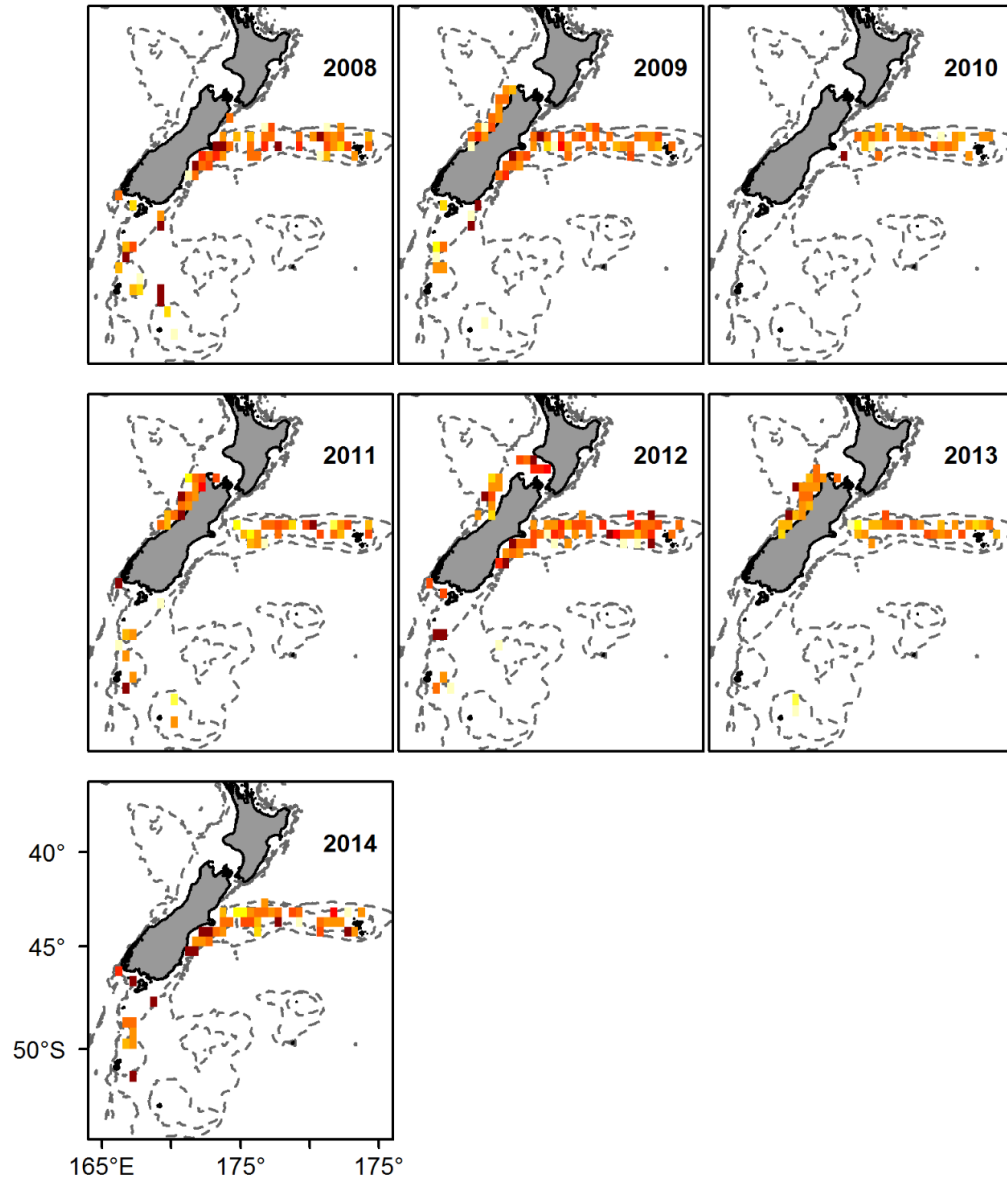
Records of female *Hydrolagus novaezealandiae* distribution between 1990-2014 found relatively high numbers on Mernoo Bank and off the South Island's Invercargill (**Fig 23**). Year by year analysis found high numbers of female *H. novaezealandiae* off South Island's western coast and the Campbell Plateau (**Fig 24**). Of 2738 tows, 484 tows were female dominated.



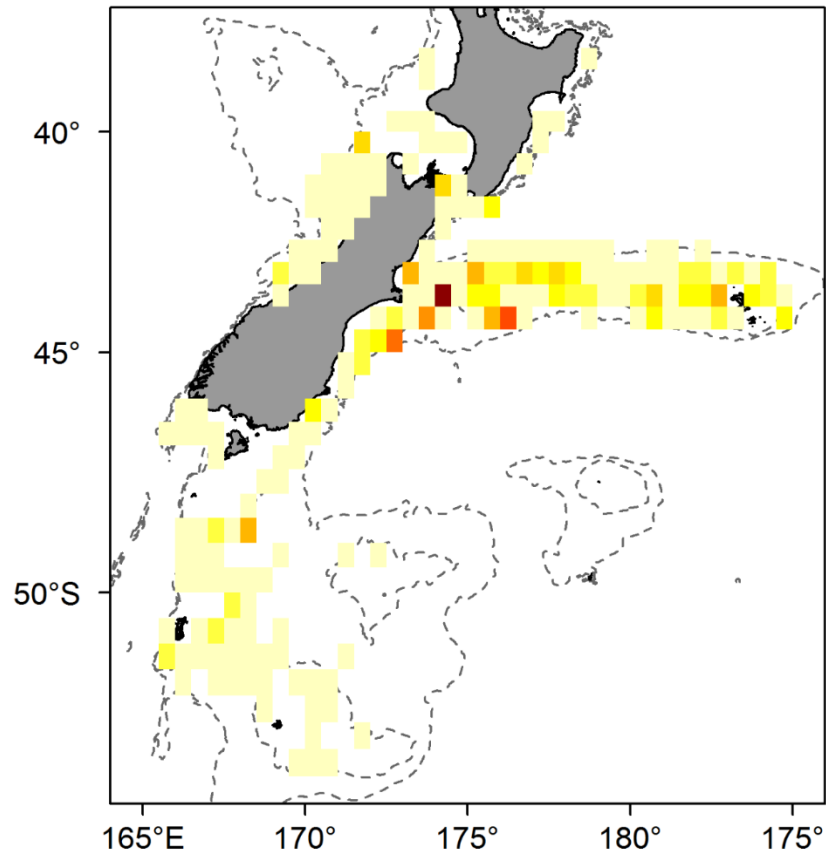
**Figure 24.** Relative distribution numbers of female *Hydrolagus novaezealandiae* that were caught and measured in research survey trawls between 1990-1998. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).



**Figure 24 (cont).** Relative distribution numbers of female *Hydrolagus novaezealandiae* that were caught and measured in research survey trawls between 1999-2007. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).



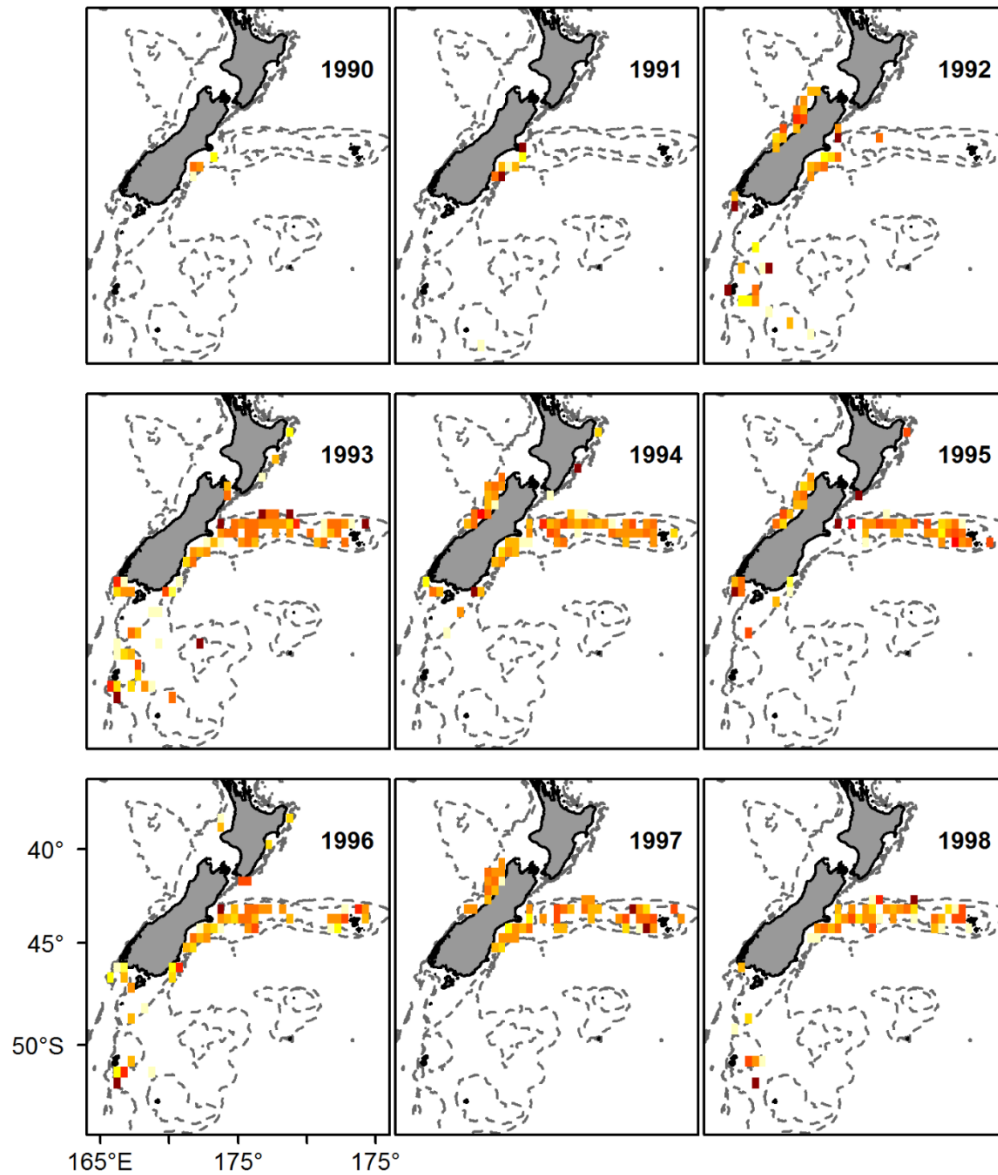
**Figure 24 (cont).** Relative distribution numbers of female *Hydrolagus novaezealandiae* that were caught and measured in research survey trawls between 2008-2014. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).



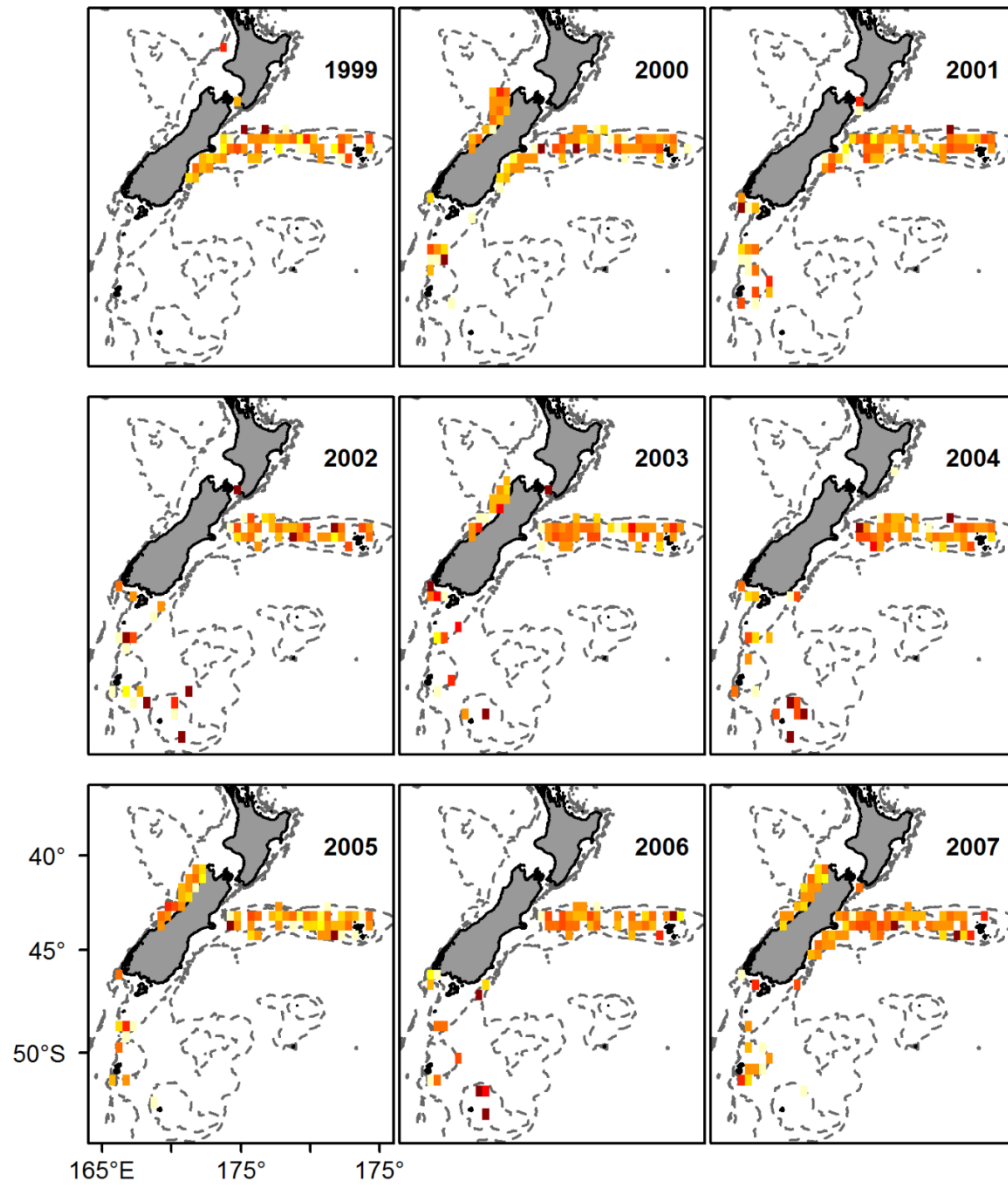
**Figure 25.** Relative distribution of number of male *Hydrolagus novaezealandiae* that were caught and measured in research survey trawls between 1990-2014. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).

Records of male *Hydrolagus novaezealandiae* distribution between 1990-2014 found relatively high numbers along the Chatham Rise, especially around Mernoo Bank (**Fig 25**). Year by year analysis (**Fig 26**) found high numbers of male *H. novaezealandiae* off South Island's western coast, along the Hikurangi Trough (year 1994, 1995, 2010) and near Campbell Island (year 1992, 1993, 2002, 2003, 2004, 2006, 2008, 2009, 2011, 2012, 2013, 2014). Of 2738 tows, 1249 tows were male dominated, with one tow meeting the criteria of a lek.

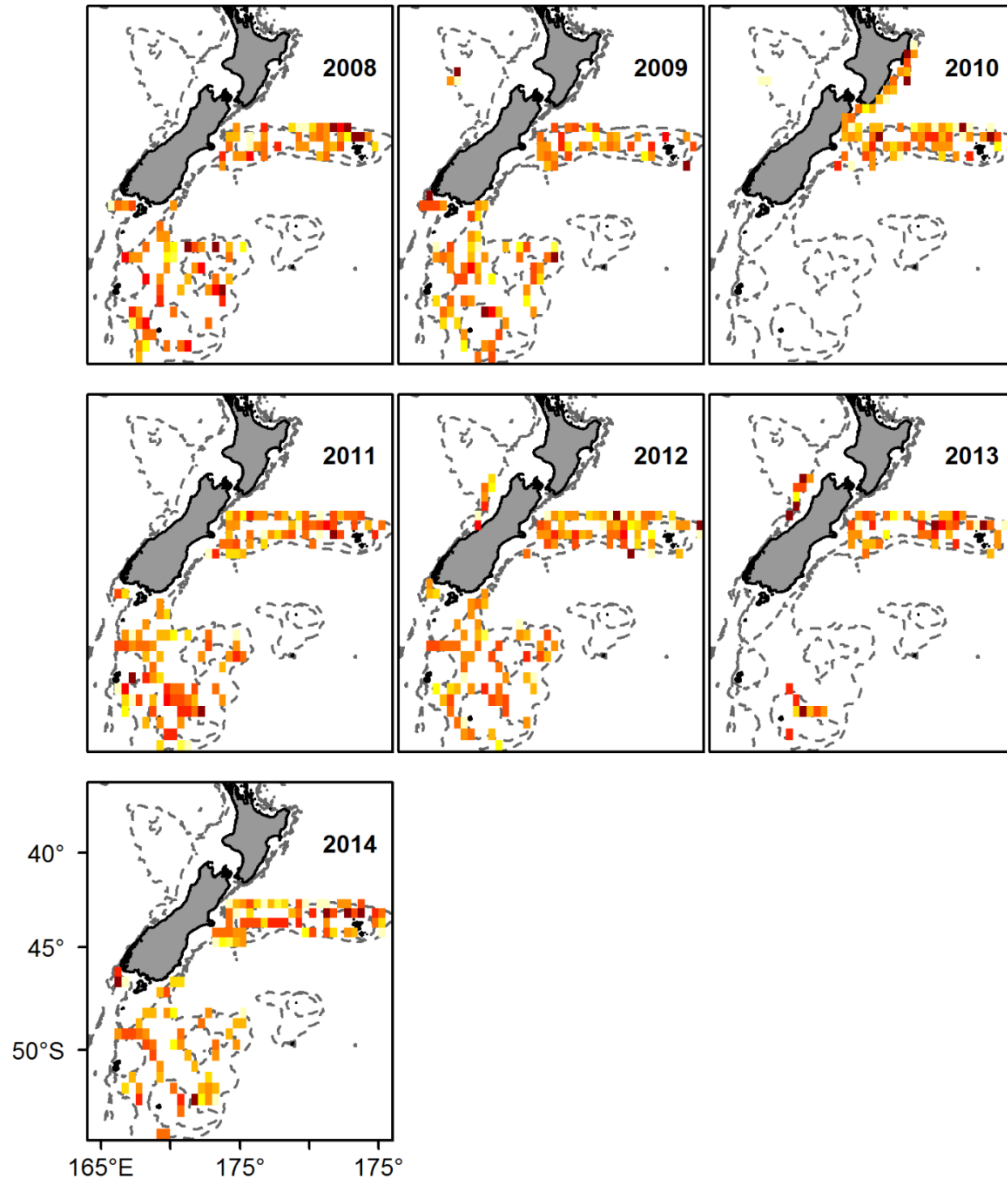




**Figure 26.** Relative distribution numbers of male *Hydrolagus novaezealandiae* that were caught and measured in research survey trawls between 1990-1998. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).



**Figure 26 (cont).** Relative distribution numbers of male *Hydrolagus novaezealandiae* that were caught and measured in research survey trawls between 1999-2007. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).



**Figure 26 (cont).** Relative distribution numbers of male *Hydrolagus novaezealandiae* that were caught and measured in research survey trawls between 2008-2014. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).

### ***Hydrolagus novaezealandiae* summary**

From 1990-2014, there was a total of 2738 tows that caught and measured *Hydrolagus novaezealandiae*. Records were within (53.44°S, 35.06°S) and (165.7°E, 184.7°E) (**Fig 17**) with a depth range of 17-1399 meters, and an average of 314.6 meters (**Fig 18**).

Of the 2738 tows, the following tows were found which matched the criteria for:

1. Pupping grounds (n=14)
2. Leks (n=45)

No tows were found that met the criteria for:

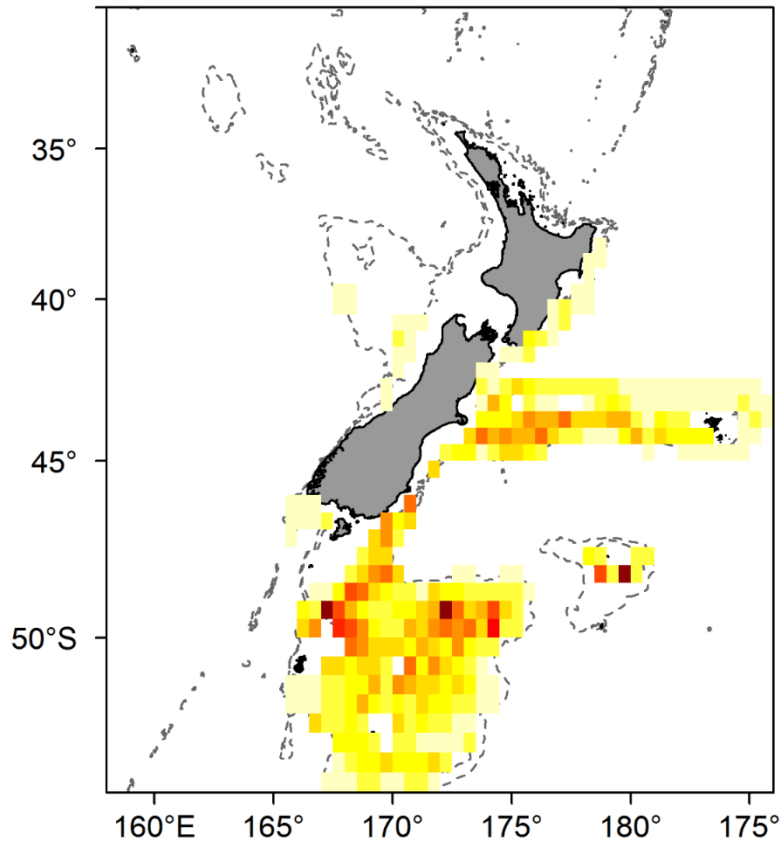
3. Nursery grounds
4. Mating grounds

Whilst aggregations occurred, data were not available to distinguish:

5. Food aggregation with possible mating
6. Exclusive foraging grounds

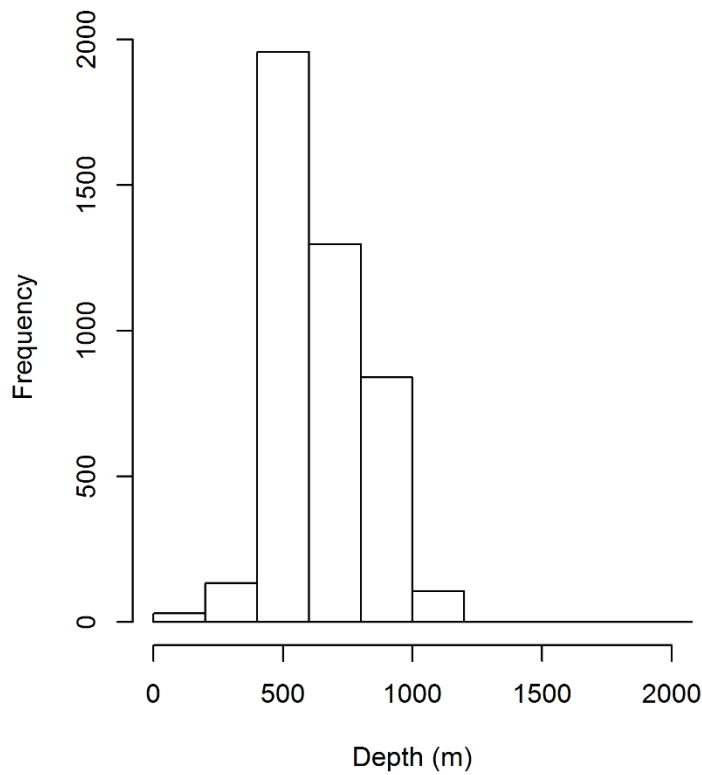
Juveniles and adults seemed to share similar mean depths (314.6 m for juveniles and 298.4 m for adults), but adults extended into deeper water (412 m maximum depth for juveniles, 750.5 maximum depth for adults). There were 1249 tows that were female-dominated (mature and juvenile) and 484 tows that were male-dominated (mature and juvenile).

**Pale Ghost Shark (Code: GSP; *Hydrolagus bemisi*)**



**Figure 27.** Relative distribution of number of *Hydrolagus bemisi* that were caught and measured in research survey trawls between 1990-2014. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).

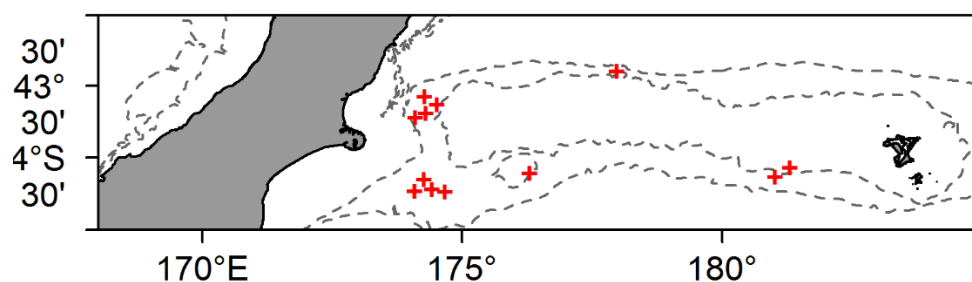
From 1990-2014, there were a total of 4377 tows where *Hydrolagus bemisi* were caught and measured (**Fig 27**). Of these tows, 95.9% of *Hydrolagus bemisi* were caught using gear code 1. Records of *Hydrolagus bemisi* were within the coordinates 54.21°S, 17.56°S – 55.3°E, 185.8°E from a minimum depth of 17 meters, maximum depth of 3678 meters, and a mean depth of 638.5 meters (**Figure 28**). Relatively high numbers of *Hydrolagus bemisi* were caught on the Campbell Plateau, near the Bounty Islands and on Chatham Rise. No *Hydrolagus bemisi* were found at the north of the North Island, and were low numbers were caught on Challenger Plateau.



**Figure 28.** Relative frequency of catch records of *Hydrolagus bemisi* by depth. Records from research survey trawls (n=4377). Depth range of overall dataset (n= 34967) 0-8468 (mean =435.2).

#### *Habitat: Pupping Locations*

Twelve of the 4377 tows satisfied the criteria (**Fig 29**). Four of these tows were of interest due to large numbers (>500) of large females (**Table 8**). These tows were repeated over a number of years in a similar area (**Fig 29, Table 8**).



**Fig 29.** The location of the four tows where the criteria were met for pupping locations of *Hydrolagus bemisi* (see also Table 8 for tows of special interest).

INDEX	DATE	DEPTH (m)	LAT (° S)	LONG (° E)	LARGE ♀	LARGE ♂
<i>tan0001_85</i>	Jan 2000	330	44.08°	175.87°	1588	140
<i>tan9901_81</i>	Jan 1999	310.5	44.18°	175.83°	1126	75
<i>tan0501_95</i>	Jan 2005	330.0	44.09°	175.87°	893	0
<i>kab1402_110</i>	June 2014	NA	44.80°	172.07°	810	0

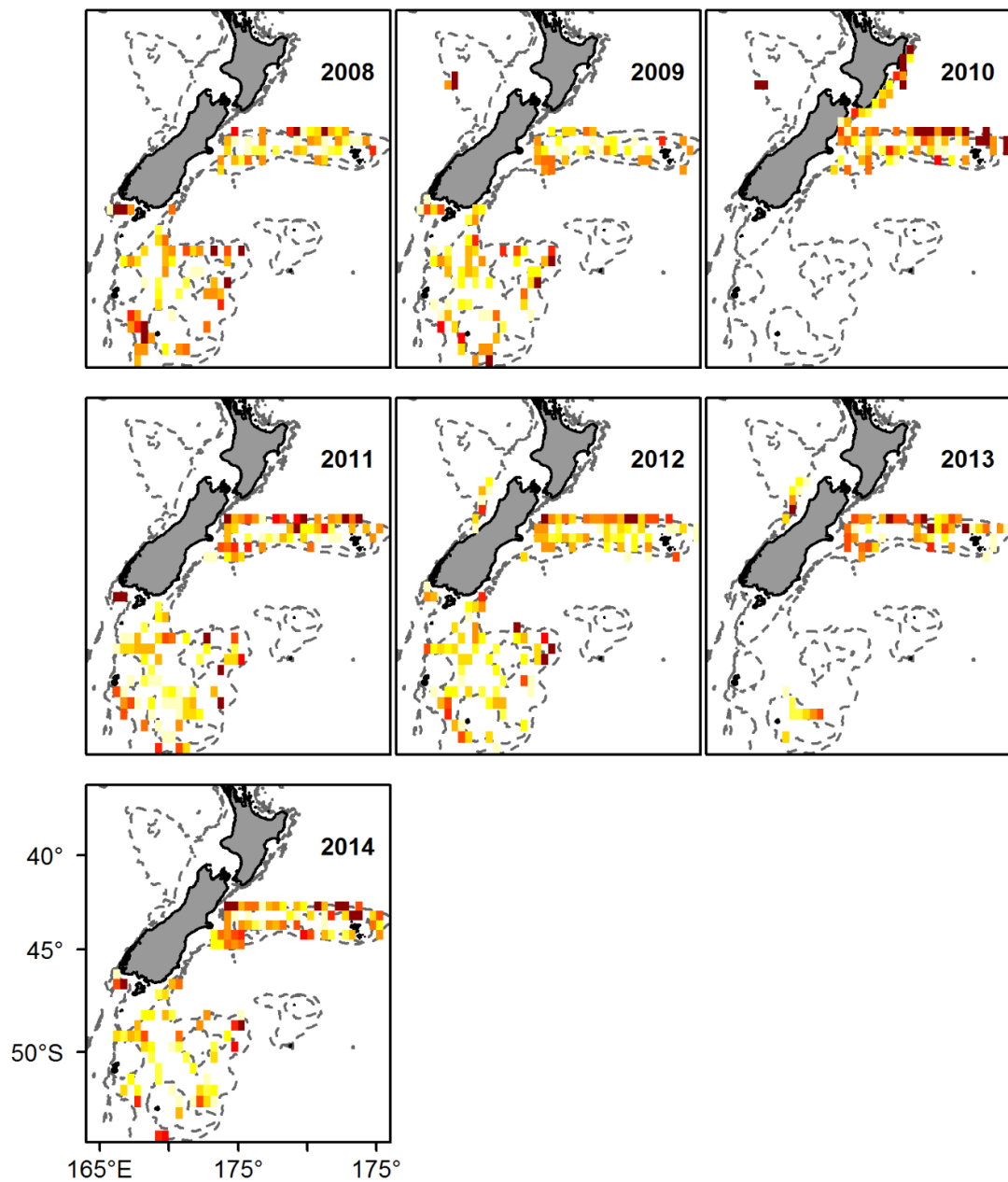
**Table 8.** Details of the four tows where criteria were met for possible pupping location tows of *Hydrolagus bemisi*.

♀ = females; ♂ = males (see also **Figure 29**).

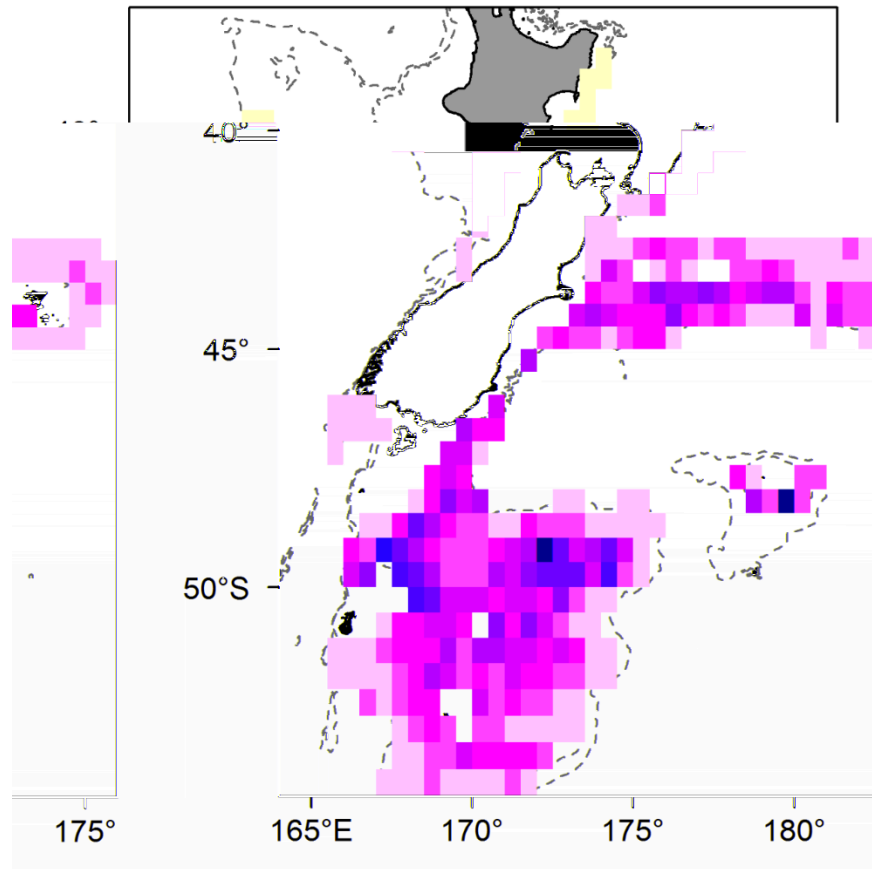






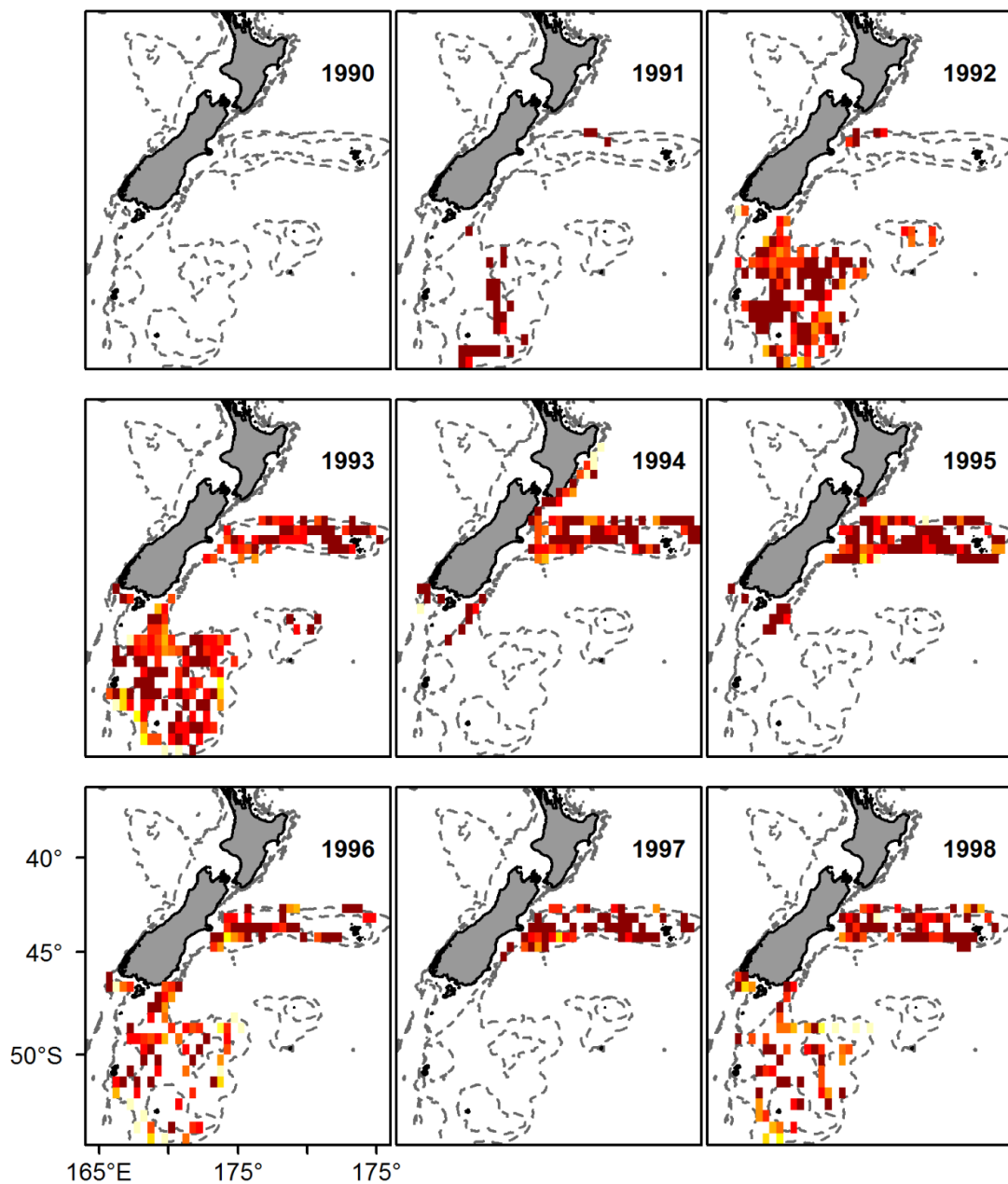


**Figure 30 (cont).** Relative distribution numbers of juvenile *Hydrolagus bemisi* that were caught and measured in research survey trawls between 2008-2014. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).

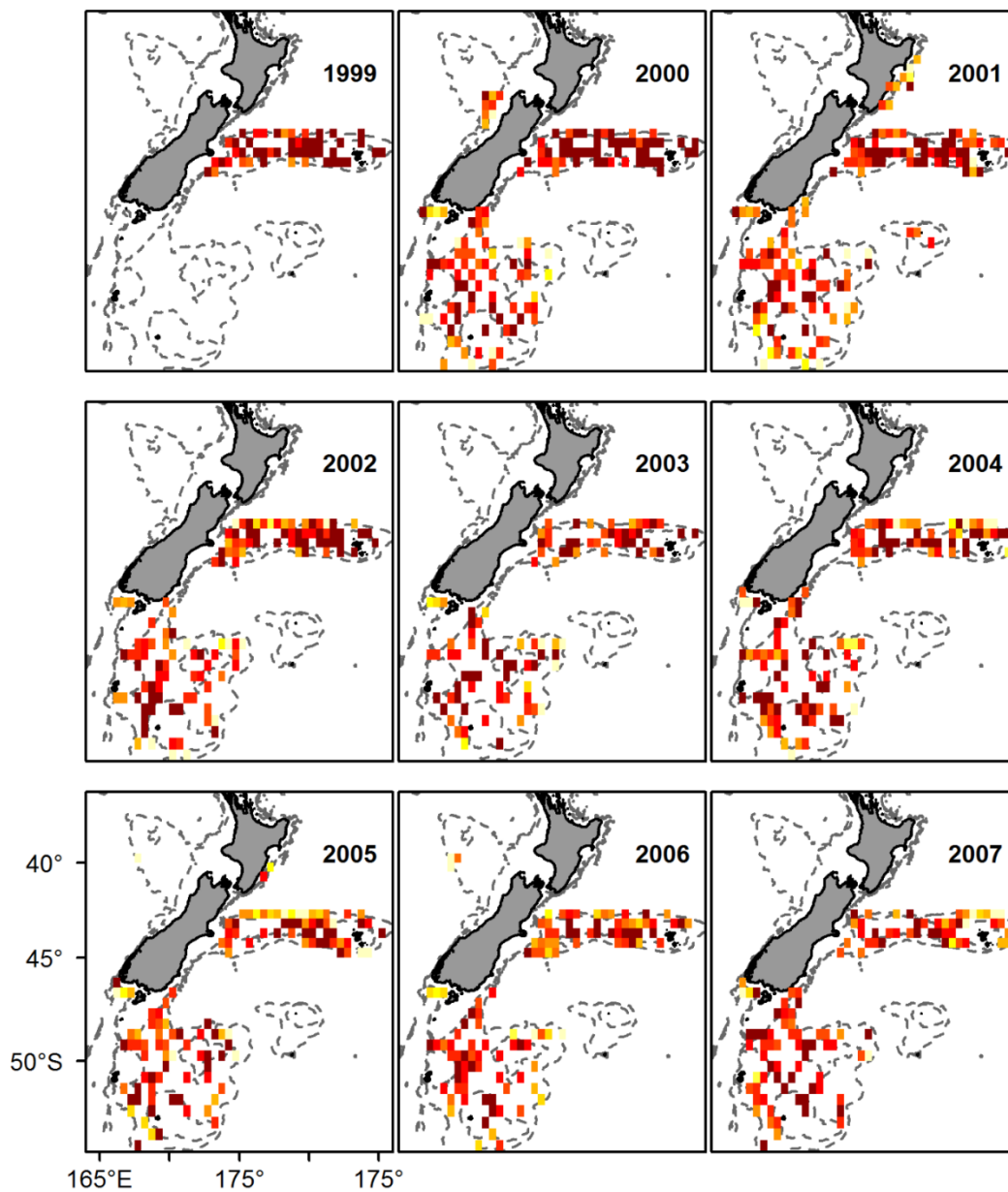


**Figure 31.** Relative distribution numbers of adult *Hydrolagus bemisi* that were caught and measured in research survey trawls between 1990-2014. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).

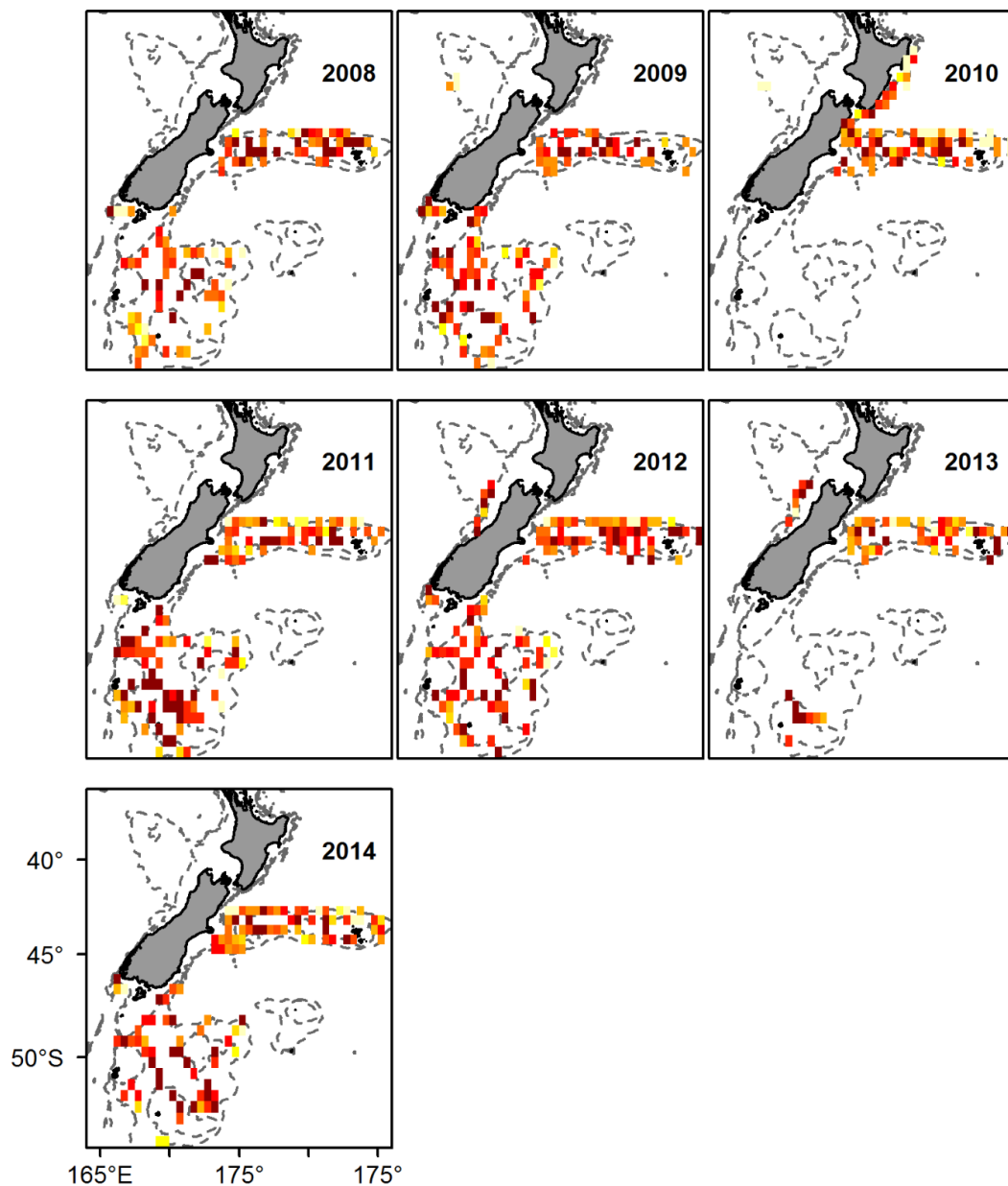
The overall distribution of adults (males and females) of *Hydrolagus bemisi* between 1990-2014 found high densities on the Chatham Rise, around the Bounty Islands and Campbell Plateau (**Fig 31**). Year by year analysis found high numbers of adults on the western coast of the South Island (year 2000, 2012, 2013) as well (**Fig 32**).



**Figure 32.** Relative distribution numbers of adult *Hydrolagus bemisi* that were caught and measured in research survey trawls between 1990-1998. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).



**Figure 32 (cont).** Relative distribution numbers of adult *Hydrolagus bemisi* that were caught and measured in research survey trawls between 1999-2007. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).



**Figure 32 (cont).** Relative distribution numbers of adult *Hydrolagus bemisi* that were caught and measured in research survey trawls between 2008-2014. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).

Average adult depth was 618 m with a minimum depth of 17 m and maximum depth of 3678 m. Adults were recorded between the coordinates 53.88° S, 17.56° S - 55.3° E, 185.8° E.

*Adult habitat: Mating Ground*

Of the 4377 total number of tows, 3906 tows met the criteria for possible mating ground. All of these tows had low single-digit individuals of each sex.

*Adult Habitat: Possible Mating Ground (Lek)*

No tows met the criteria for a lek.

*Adult Habitat: Possible Mating Ground (Aggregation)*

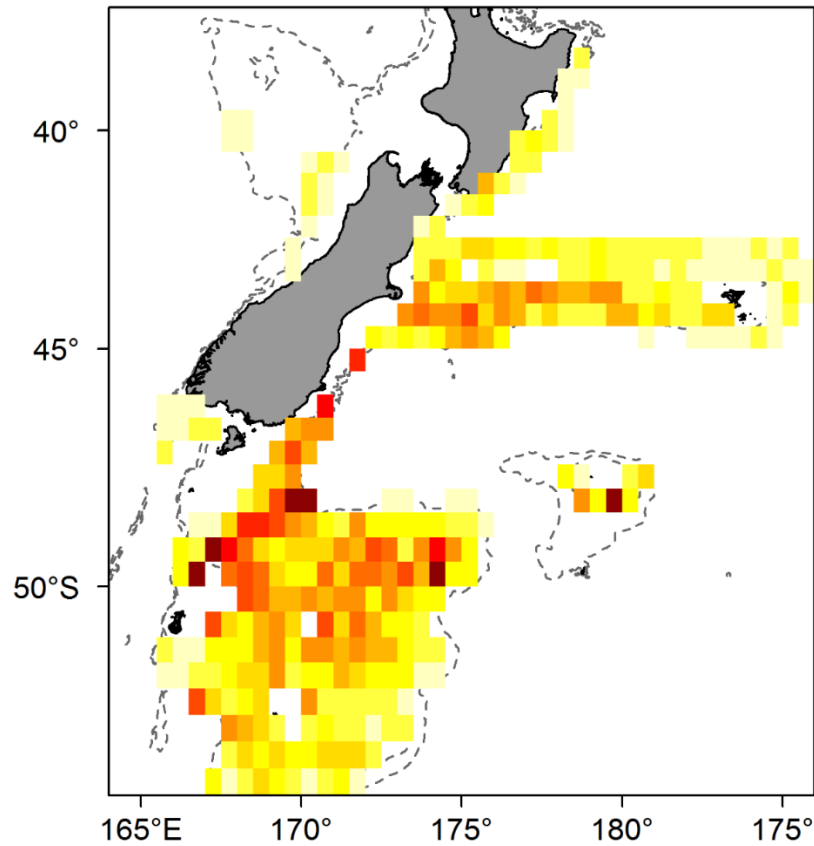
No tows met the criteria for a mating aggregation.

*Adult Habitat: Food Aggregation with Possible Mating*

We could not detect any food aggregation with possible mating (see Methods).

*Adult Habitat: Exclusive Foraging Ground*

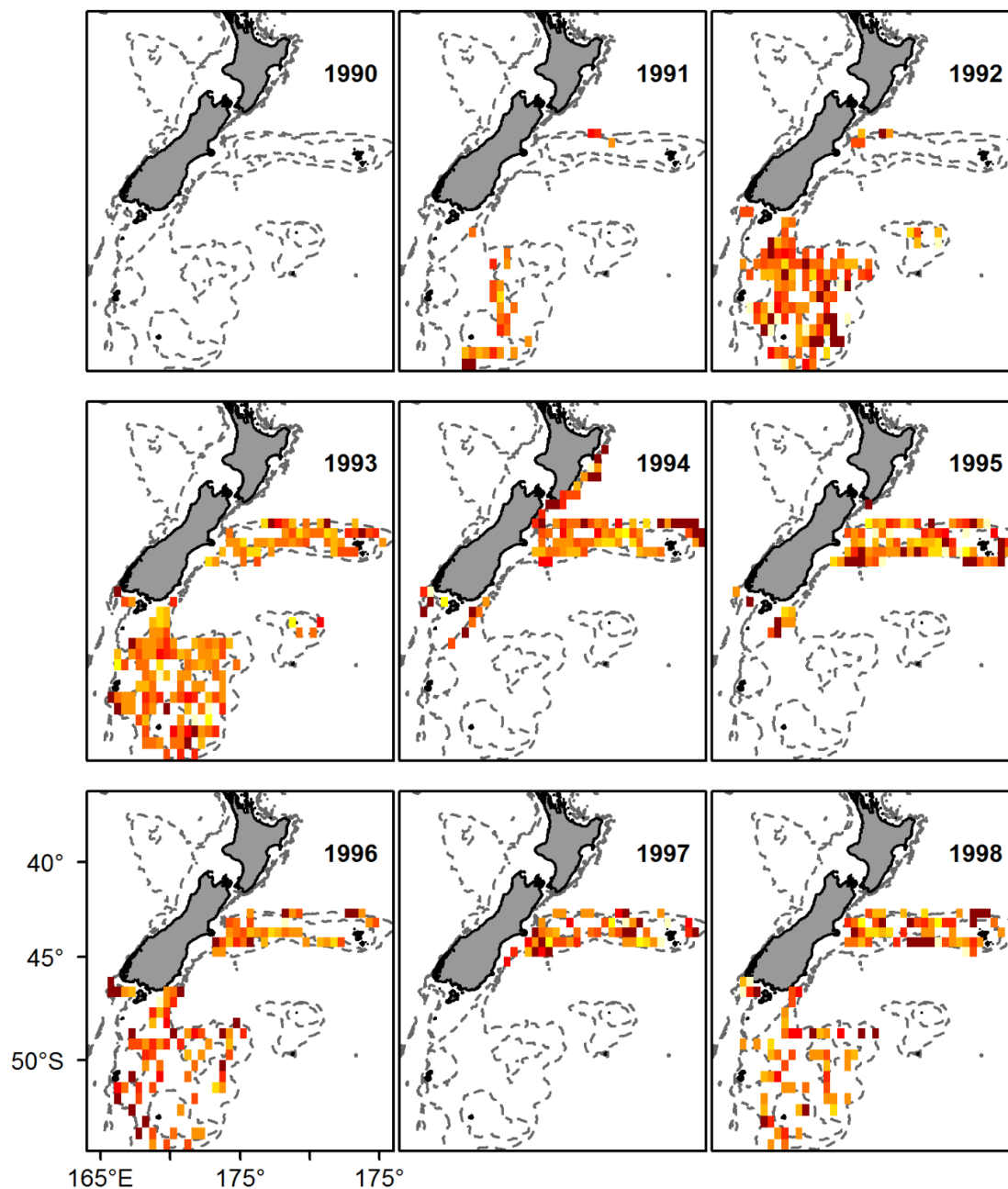
We could not detect an exclusive foraging ground (see Methods).



**Figure 33.** Relative distribution of number of female *Hydrolagus bemisi* that were caught and measured in research survey trawls between 1990-2014. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).

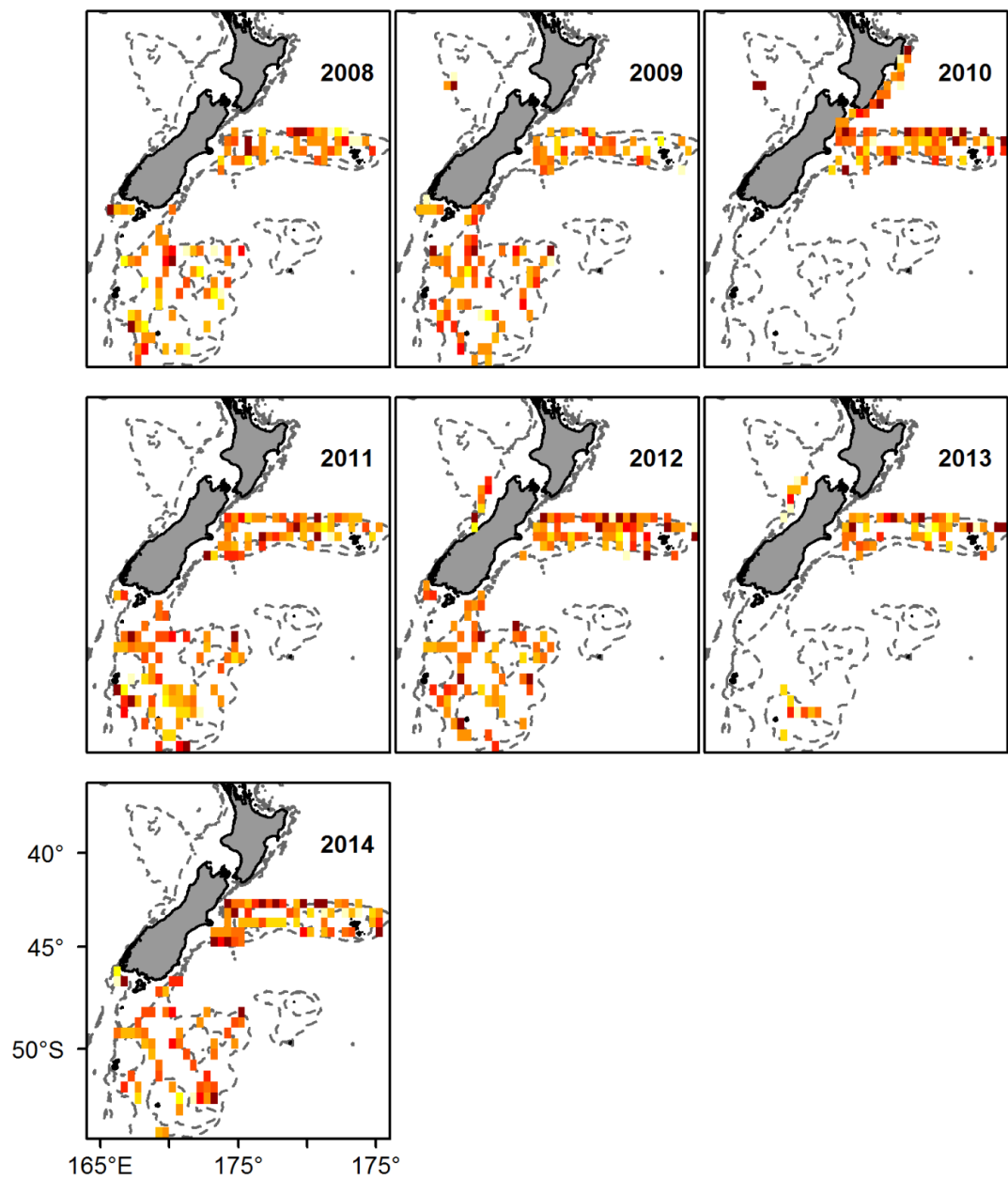
Records of female *Hydrolagus bemisi* distribution between 1990-2014 found relatively high numbers off of the South Island's Campbell Plateau shelf and Chatham Rise, especially around Mernoo Bank, and the Bounty Islands (**Fig 33**). Year by year analysis found high numbers of female *H. novaezealandiae* at the edge of the Challenger Plateau (year 2006, 2009, 2010; **Fig 34**). Of 4377 tows, 820 tows were female dominated.



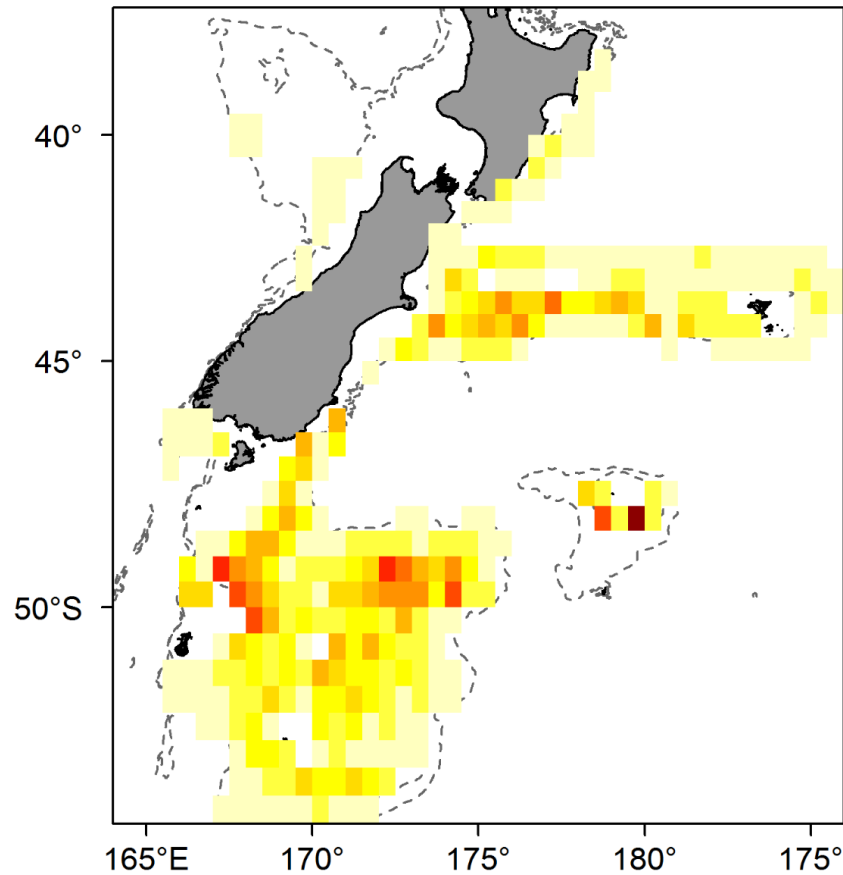


**Figure 34.** Relative distribution numbers of female *Hydrolagus bemisi* that were caught and measured in research survey trawls between 1990-1998. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).



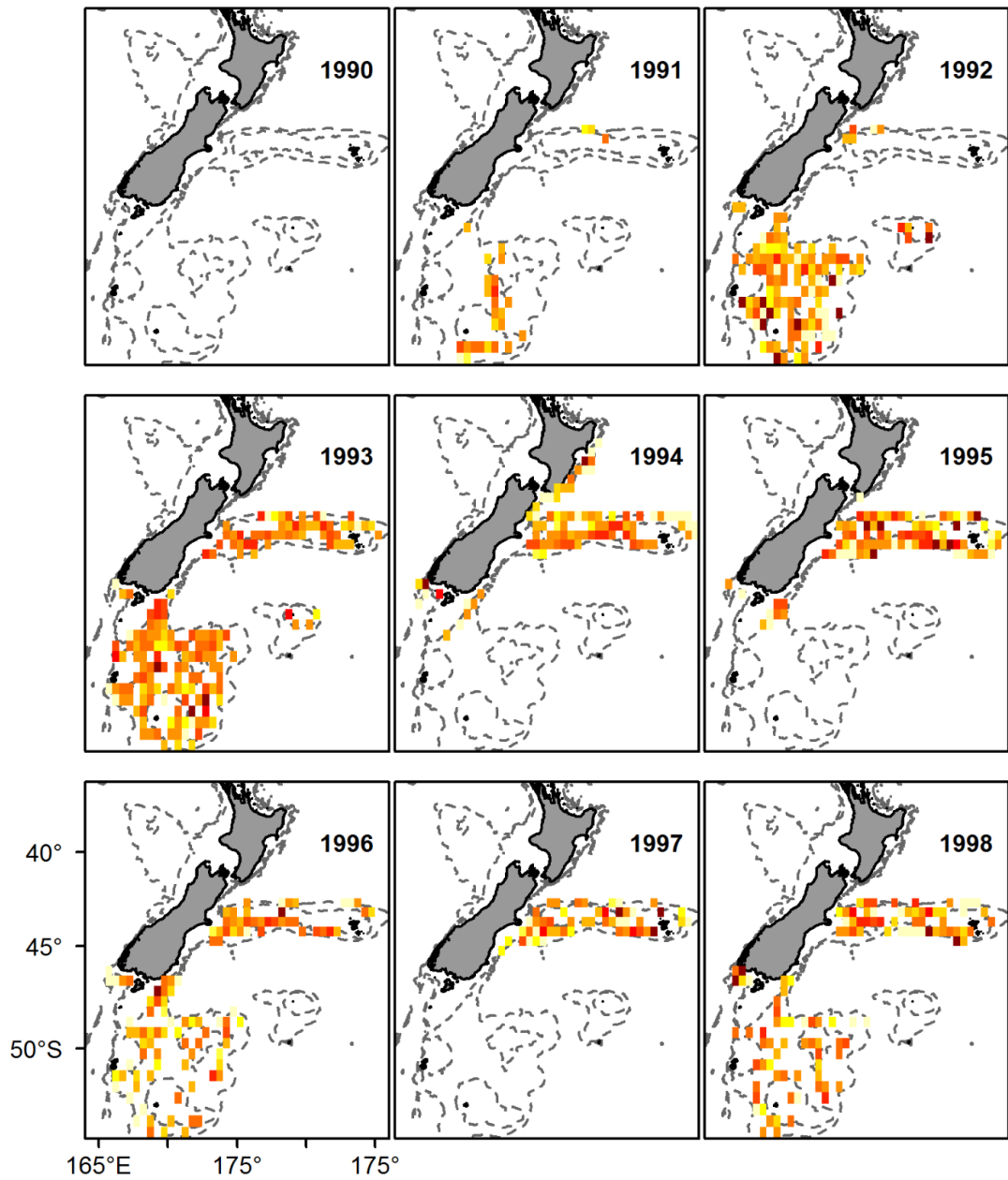


**Figure 34 (cont).** Relative distribution numbers of female *Hydrolagus bemisi* that were caught and measured in research survey trawls between 2008-2014. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).

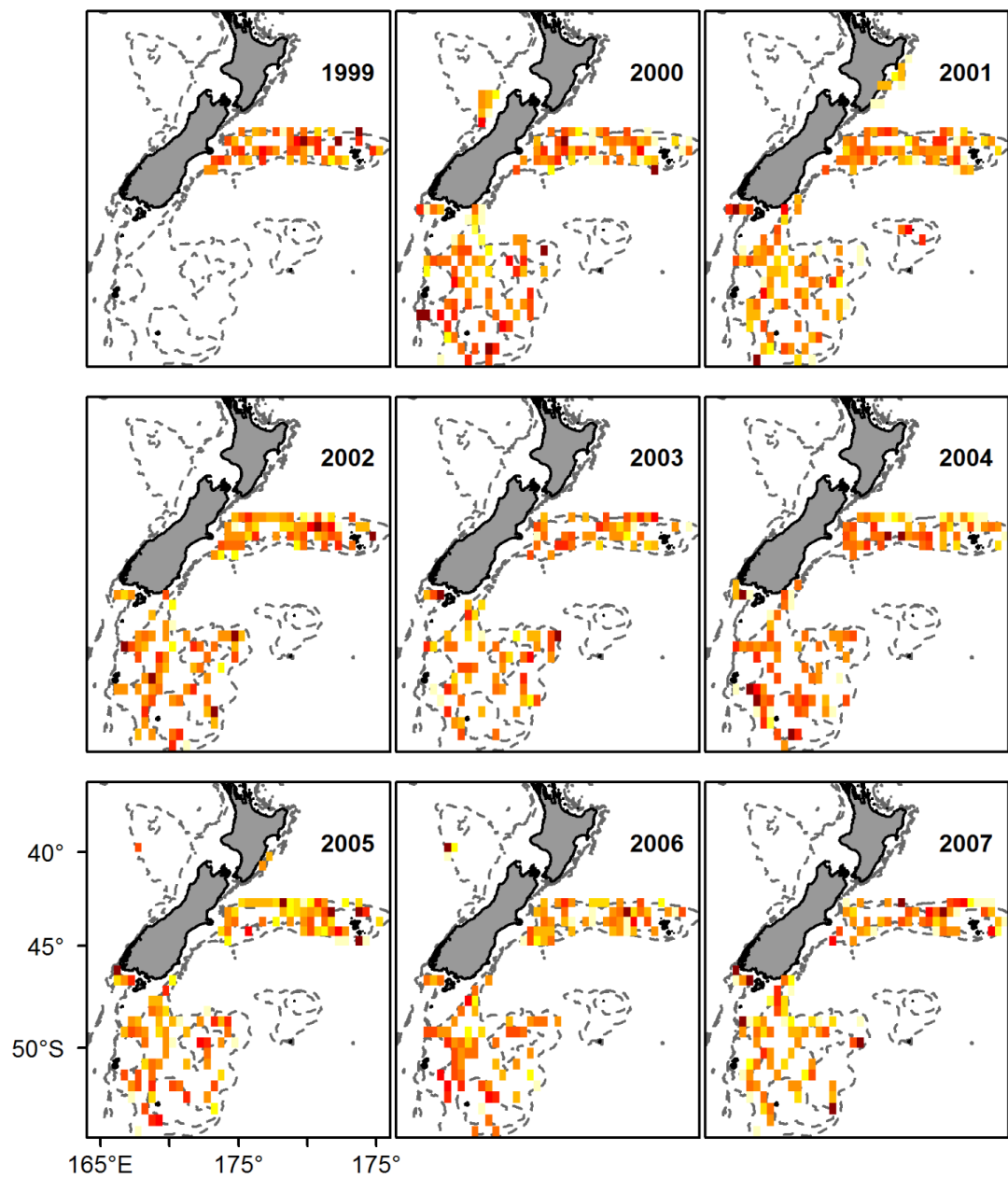


**Figure 35.** Relative distribution of number of male *Hydrolagus bemisi* that were caught and measured in research survey trawls between 1990-2014. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).

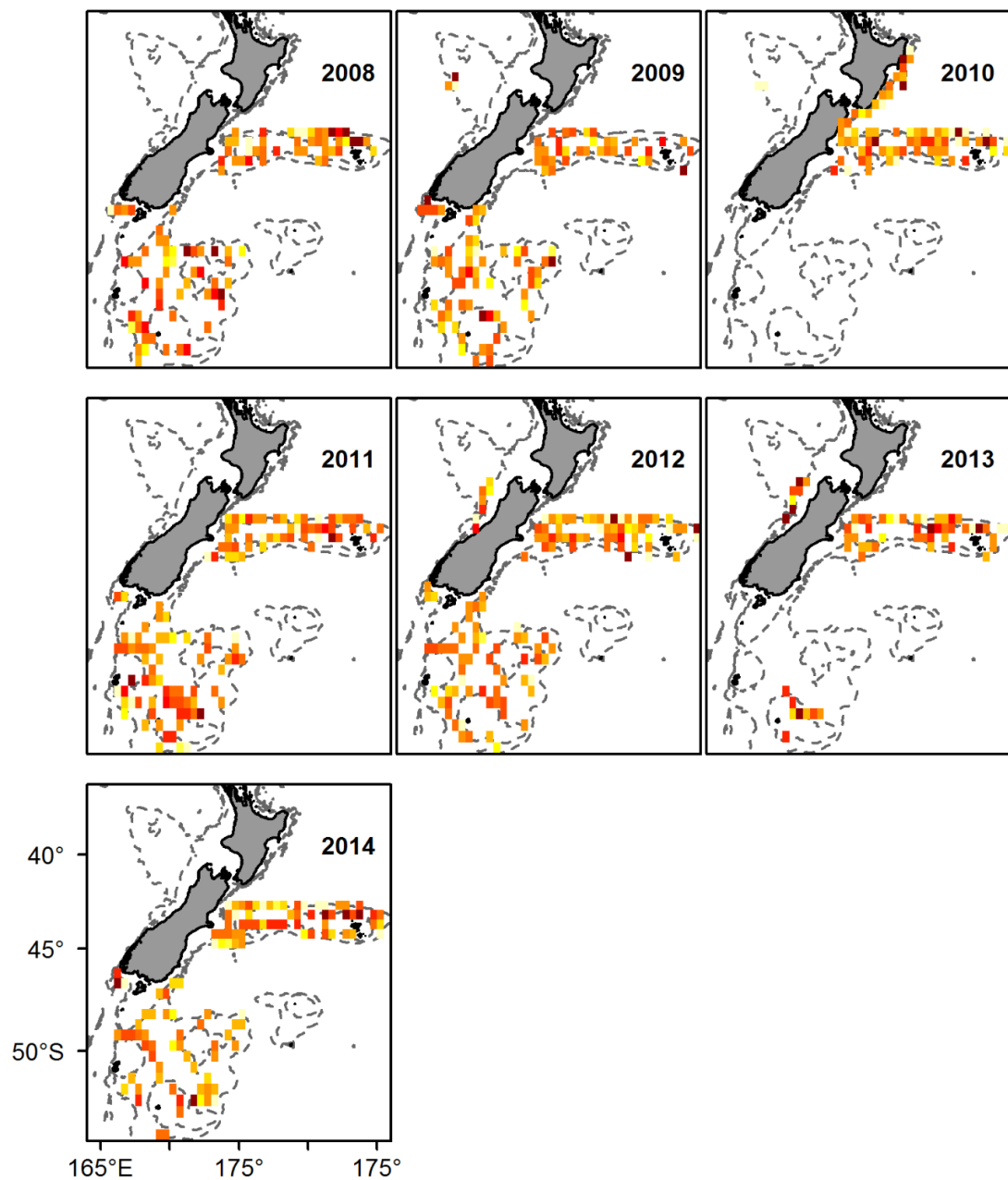
Records of male *Hydrolagus bemisi* distribution between 1990-2014 found relatively high numbers along the Chatham Rise, especially around Mernoo Bank, on the Campbell Plateau, and the Bounty Islands (**Fig 35**). Year by year analysis (**Fig 36**) found high numbers of male *H. bemisi* off South Island's western coast (year 2000, 2012, 2013) and along the Hikurangi Trough (year 1994, 2001, 2005, 2010). Of 4377 tows, 3231 tows were male dominated, but none met the criteria of a lek.



**Figure 36.** Relative distribution numbers of male *Hydrolagus bemisi* that were caught and measured in research survey trawls between 1990-1998. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).



**Figure 36 (cont).** Relative distribution numbers of male *Hydrolagus bemisi* that were caught and measured in research survey trawls between 1999-2007. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).



**Figure 36 (cont).** Relative distribution numbers of male *Hydrolagus bemisi* that were caught and measured in research survey trawls between 2008-2014. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).

### ***Hydrolagus bemisi* summary**

From 1990-2014, there was a total of 4377 tows that caught and measured *Hydrolagus bemisi*. Records were within (54.21°S, 17.56°S) and (55.3°E, 185.8°E) (**Fig 27**) with a depth range of 17-3678 meters, and an average of 638.5 meters (**Fig 28**).

Of the 4377 tows, the following tows were found which matched the criteria for:

1. Pupping grounds (n=12)
2. Mating grounds (n=3906)

No tows were found that met the criteria for:

3. Nursery grounds
4. Leks

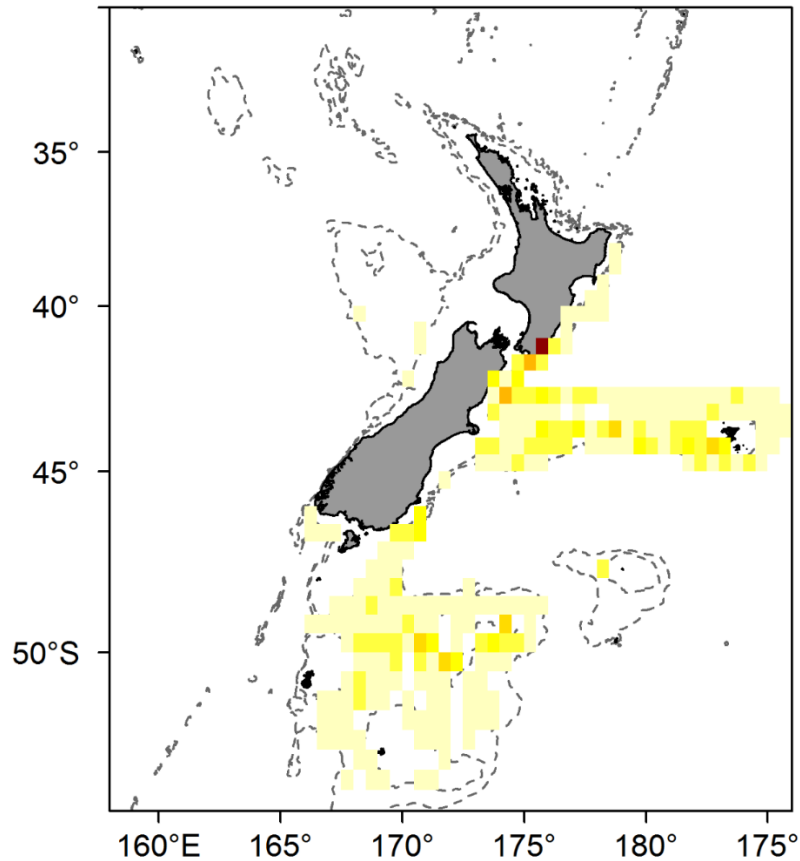
Whilst aggregations occurred, data were not available to distinguish:

5. Food aggregation with possible mating
6. Exclusive foraging grounds

The relative occurrence of *Hydrolagus bemisi* is less patchy than other Chondrichthyans, with high densities being found around the Auckland Islands, Bounty Islands, Pukaki Rise and on Chatham Rise. Juveniles and adults seemed to share similar mean depths (614.8 m for juveniles and 704.1 m for adults), but adults extended into deeper water (704.1 m maximum depth for juveniles, 3678 maximum depth for adults). There were 820 tows that were female-dominated (mature and juvenile) and 3231 tows that were male-dominated (mature and juvenile).

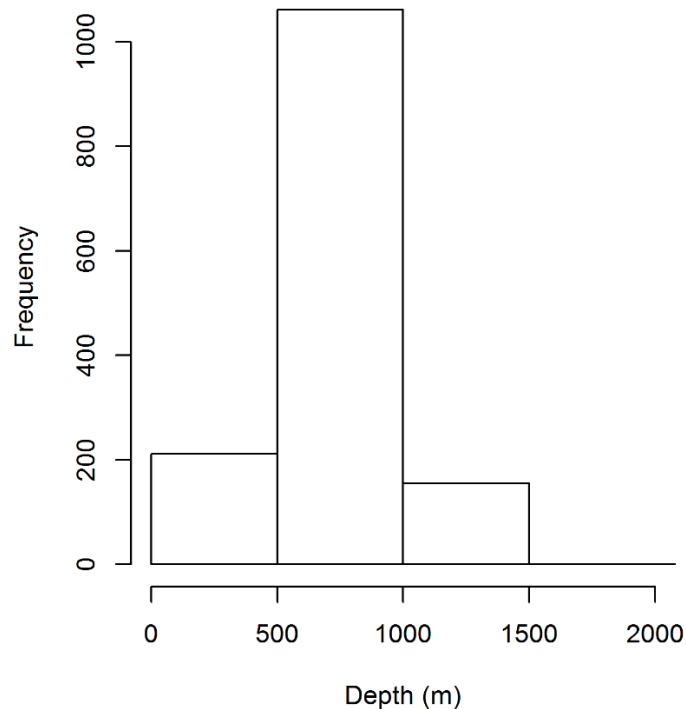


Longnose Spookfish (Code: LCH; *Harriotta raleighana*)



**Figure 37.** Relative distribution of number of *Harriotta raleighana* that were caught and measured in research survey trawls between 1990-2014. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).

From 1990-2014, there were a total of 1430 tows where *Harriotta raleighana* were caught and measured (**Fig 37**). Of these tows, 87% of *Harriotta raleighana* were caught using gear code 1. Records of *Harriotta raleighana* were within the coordinates 53.47°S, 35.99°S – 166.2°E, 185.9°E from a minimum depth of 17 meters, maximum depth of 3678 meters, and a mean depth of 731.7 meters (**Fig 38**). Relatively high numbers of adult *Harriotta raleighana* were caught near North Island's Flat Point (dark red square; **Fig 37**).



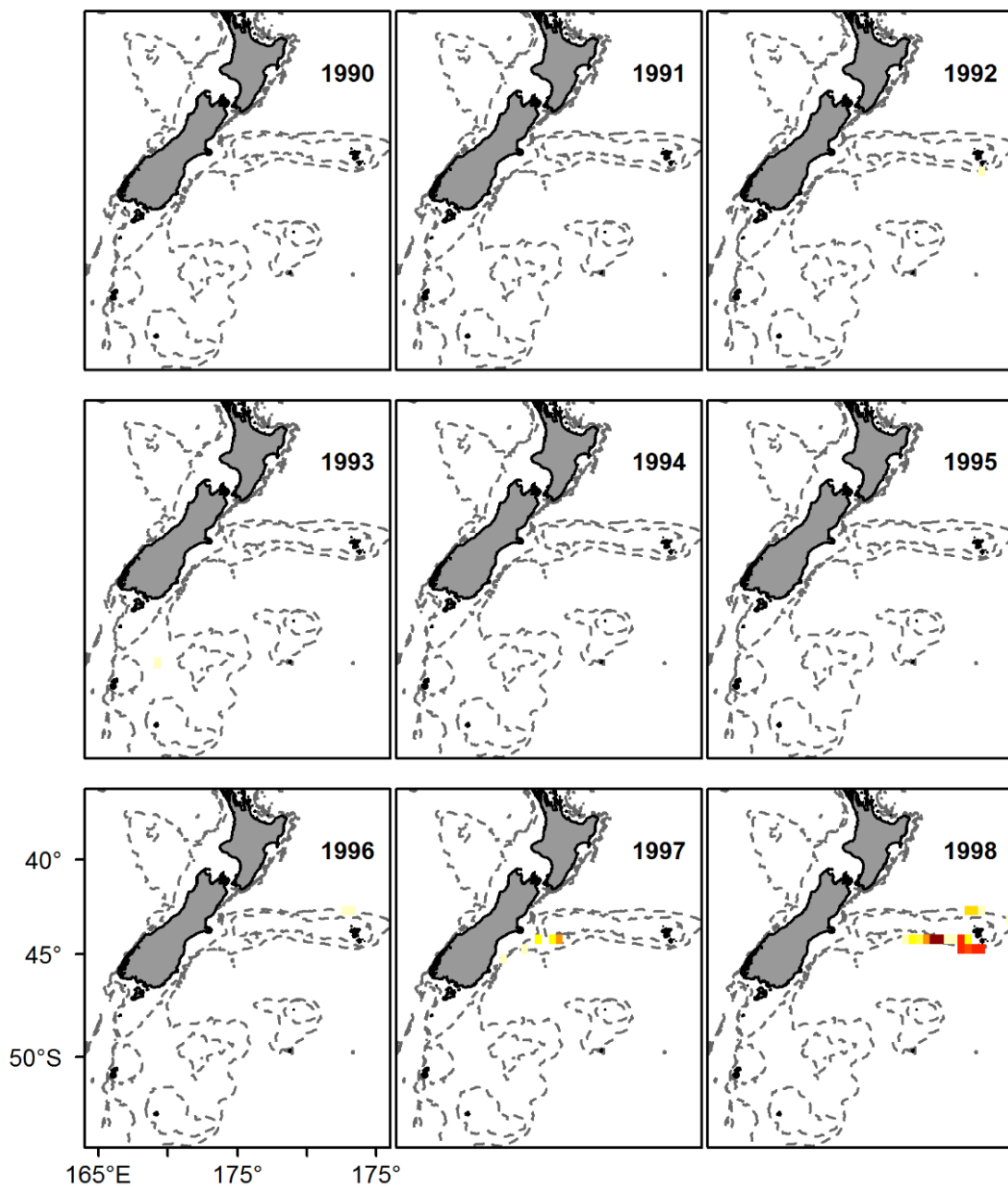
**Figure 38.** Relative frequency of catch records of *Harriotta raleighana* by depth. Records from research survey trawls (n=1430). Depth range of overall dataset (n= 34967) 0-8468 (mean =435.2).

#### *Habitat: Pupping Locations*

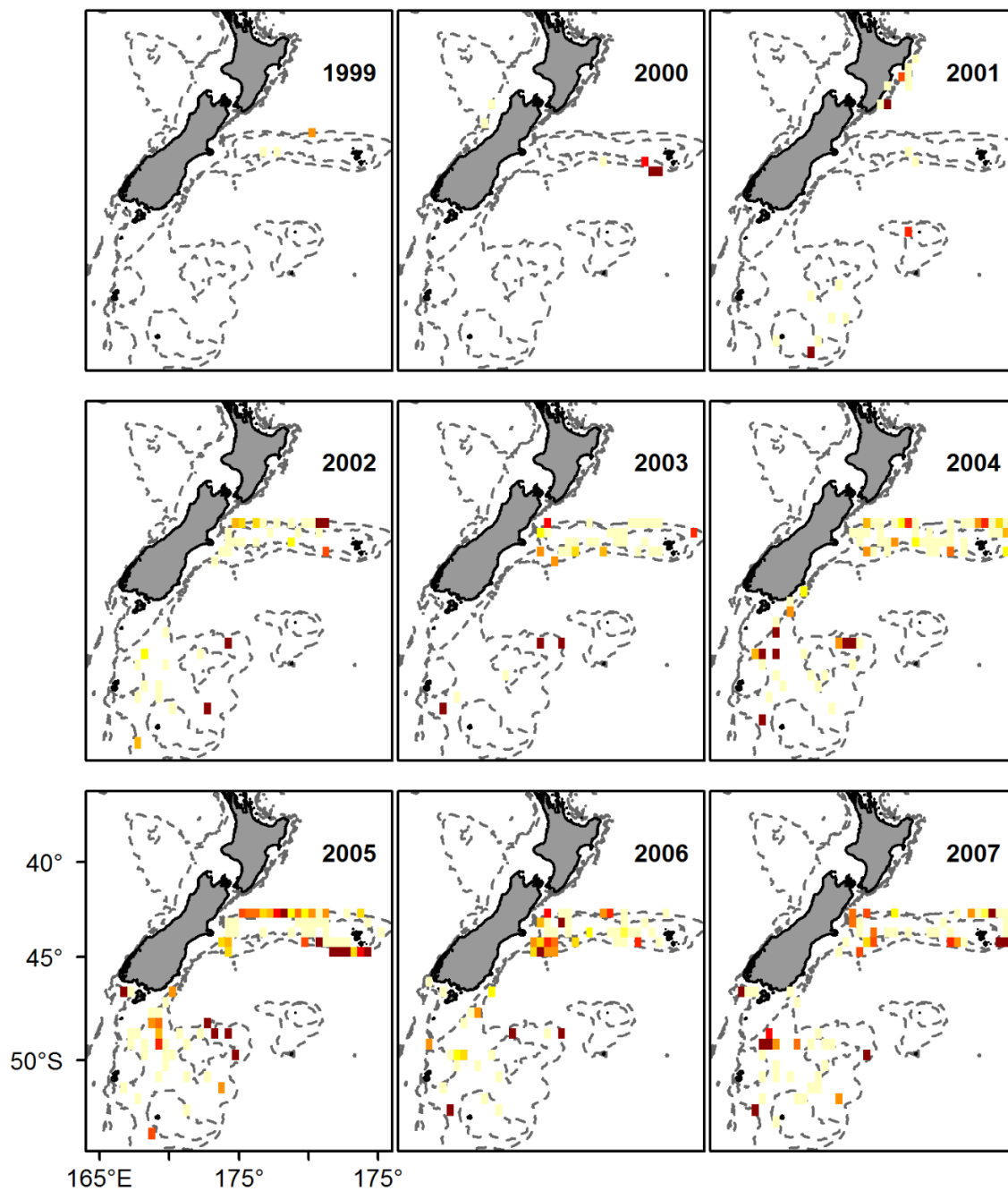
No tows met the criteria for a pupping location.

#### *Juvenile Habitat: Nurseries*

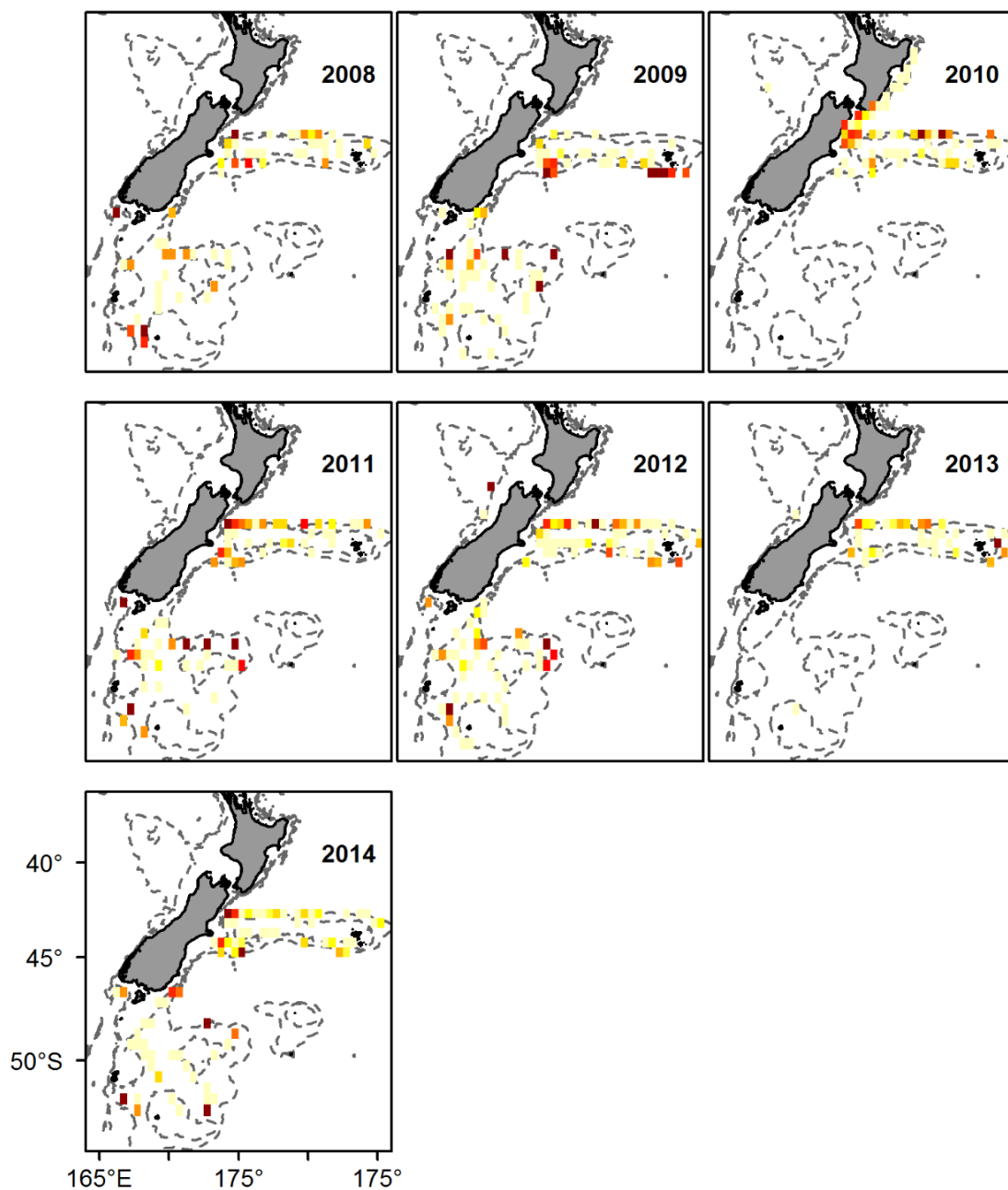
There were no tows which met the criteria for nursery grounds, although there were high densities of juveniles caught on Chatham Rise, especially west of Mernoo Bank and around the Chatham Islands (**Fig 39**). However, these tows always had high numbers of adult females and males. Average juvenile depth was 714.7 m with a maximum depth of 888 m and minimum depth of 17 m. Records were between the coordinates 53.47° S, 38.51° S - 166.2° E, 185.9° E.



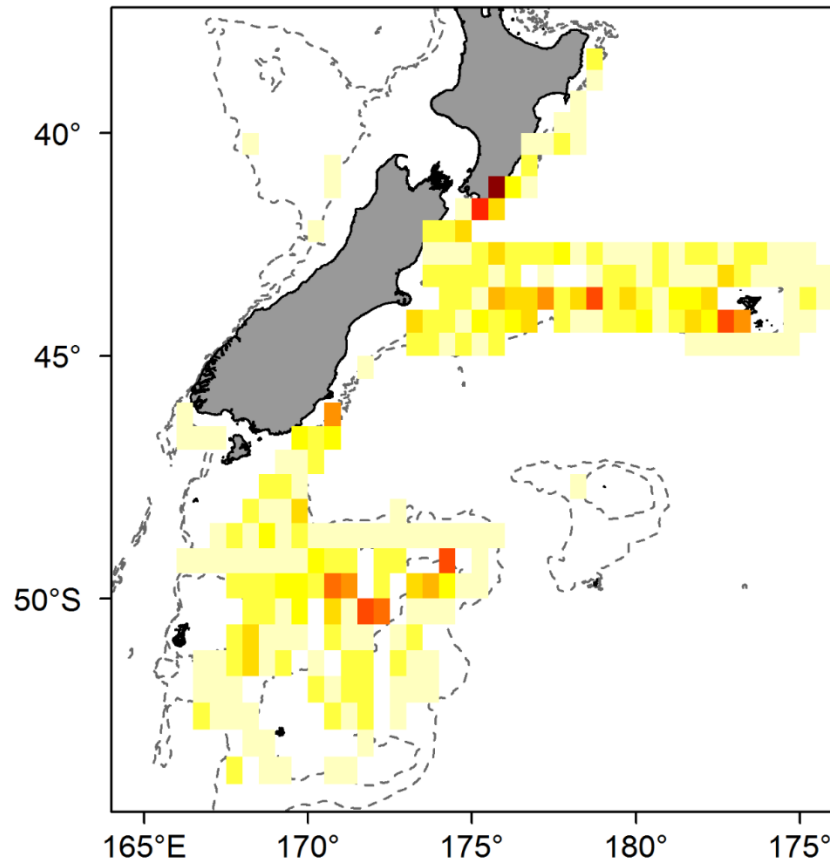
**Figure 39.** Relative distribution numbers of juvenile *Harriotta raleighana* that were caught and measured in research survey trawls between 1990-1998. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).



**Figure 39 (cont).** Relative distribution numbers of juvenile *Harriotta raleighana* that were caught and measured in research survey trawls between 1999-2007. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).

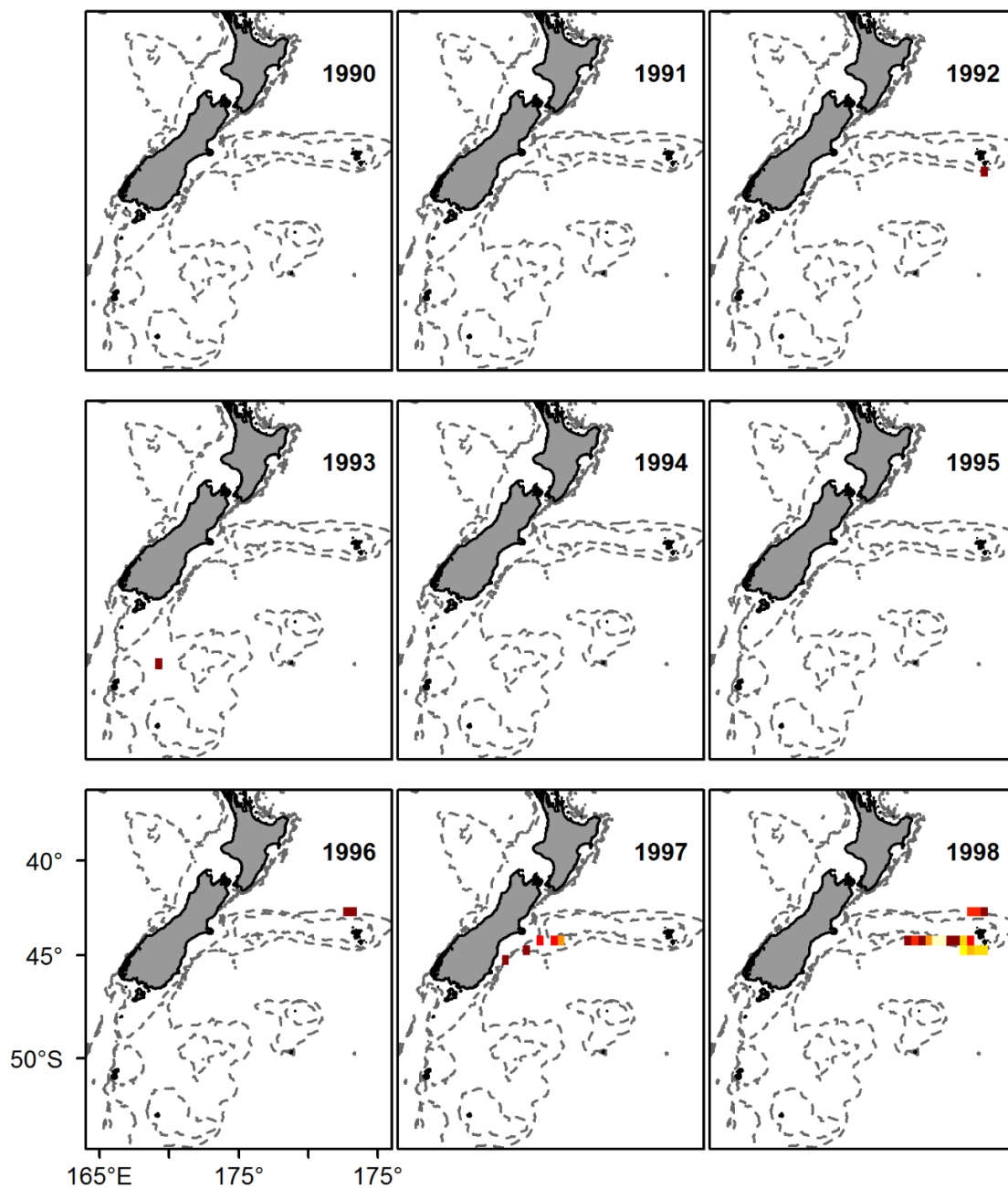


**Figure 39 (cont).** Relative distribution numbers of juvenile *Harriotta raleighana* that were caught and measured in research survey trawls between 2008-2014. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).

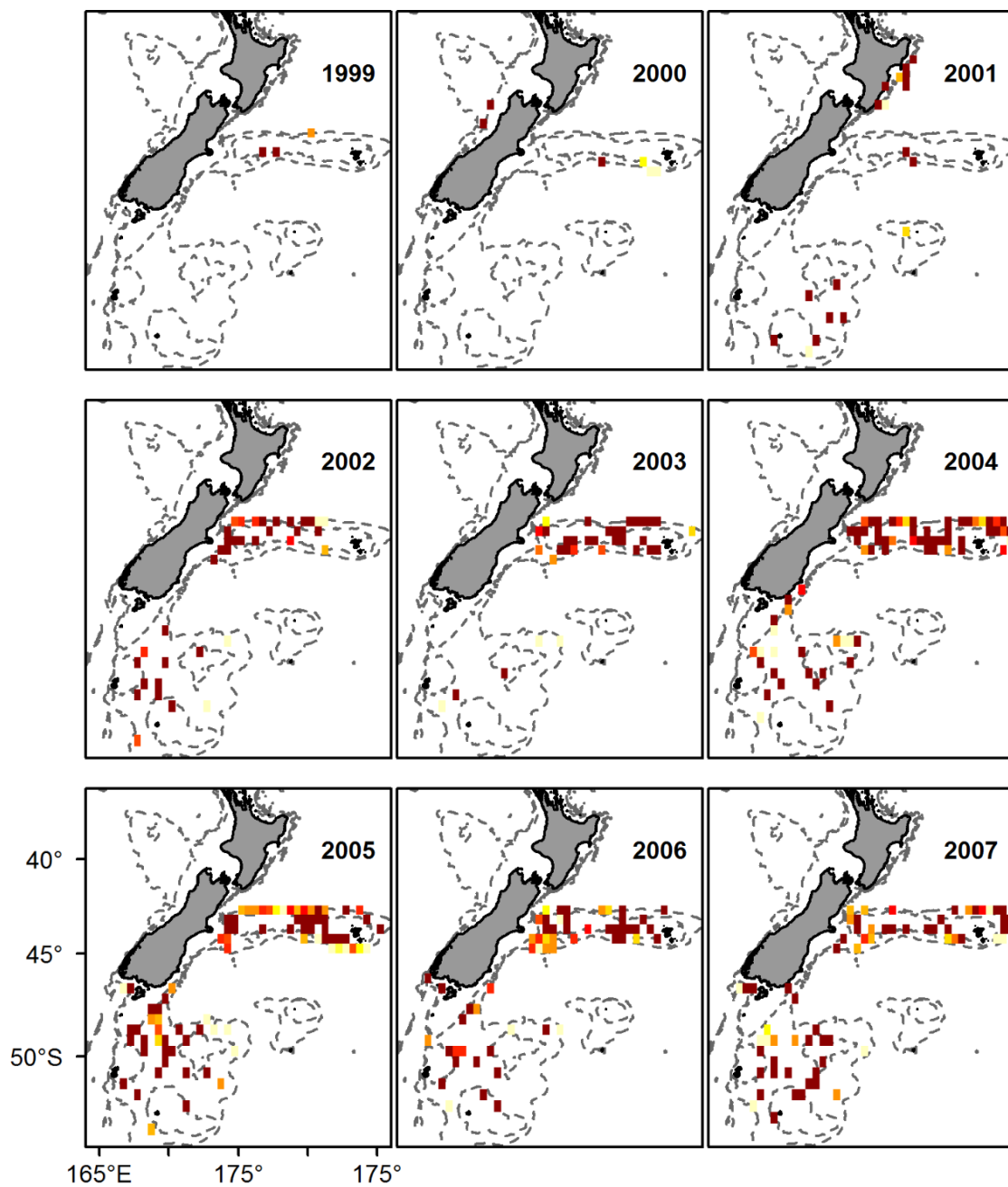


**Figure 40.** Relative distribution numbers of adult *Harriotta raleighana* that were caught and measured in research survey trawls between 1990-2014. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).

The overall distribution of adults (males and females) of *Harriotta raleighana* between 1990-2014 found high densities on the Chatham Rise, on the Campbell Plateau, and off North Island's Flat Point (**Fig 40**). Year by year analysis found high numbers of adults on the Chatham Rise and Campbell Plateau (**Fig 41**).

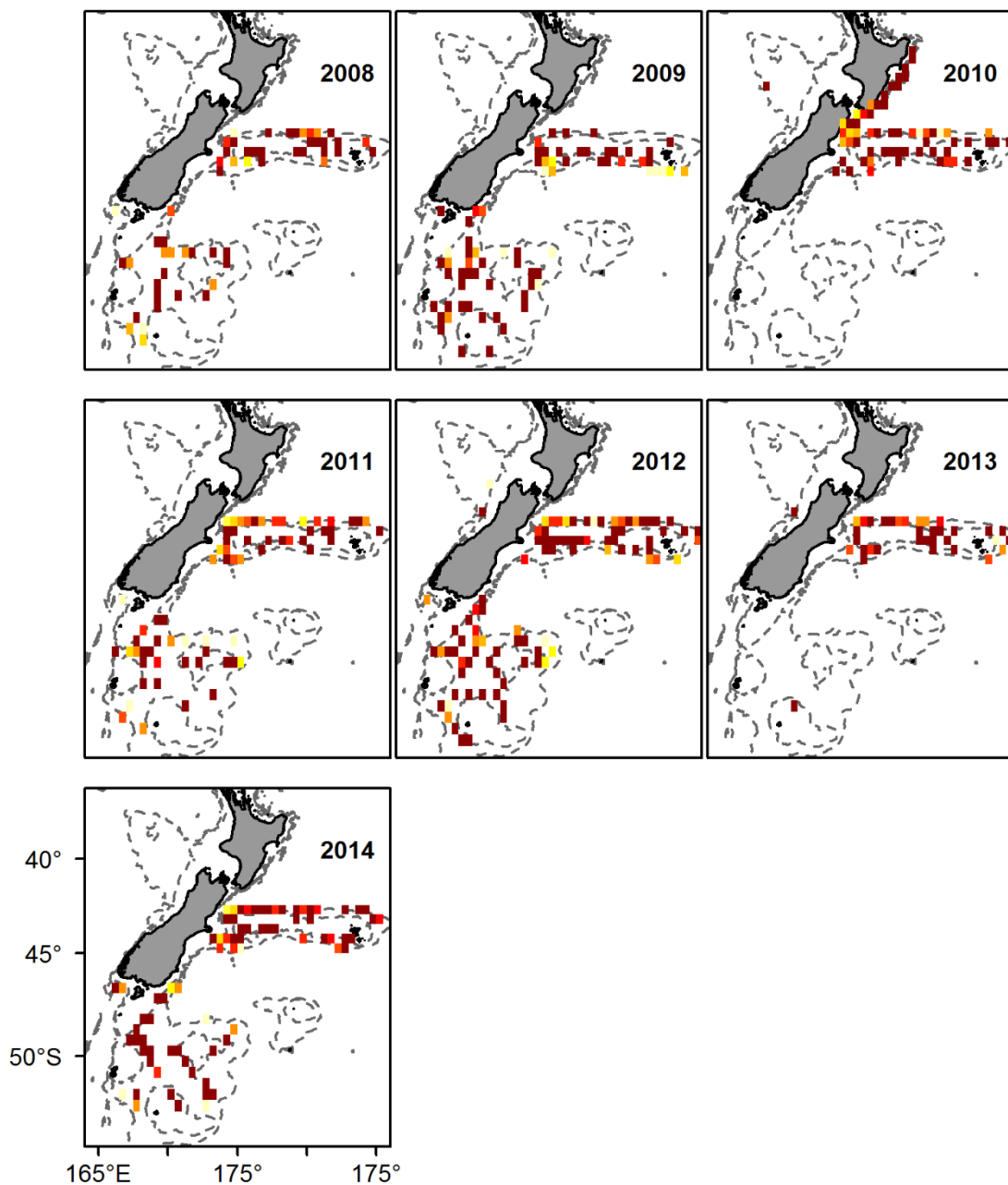


**Figure 41.** Relative distribution numbers of adult *Harriotta raleighana* that were caught and measured in research survey trawls between 1990-1998. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).



**Figure 41 (cont).** Relative distribution numbers of adult *Harriotta raleighana* that were caught and measured in research survey trawls between 1999-2007. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).





**Figure 41 (cont).** Relative distribution numbers of adult *Harriotta raleighana* that were caught and measured in research survey trawls between 2008-2014. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).

Average adult depth was 656.5 m with a minimum depth of 17 m and maximum depth of 3678 m. Adults were recorded between the coordinates 53.39° S, 36.02° S - 166.2° E, 185.9° E.

*Adult habitat: Mating Ground*

Of the 1430 total number of tows, 1218 tows met the criteria for possible mating ground. All of these tows had low single-digit individuals of each sex.

*Adult Habitat: Possible Mating Ground (Lek)*

No tows met the criteria for a lek.

*Adult Habitat: Possible Mating Ground (Aggregation)*

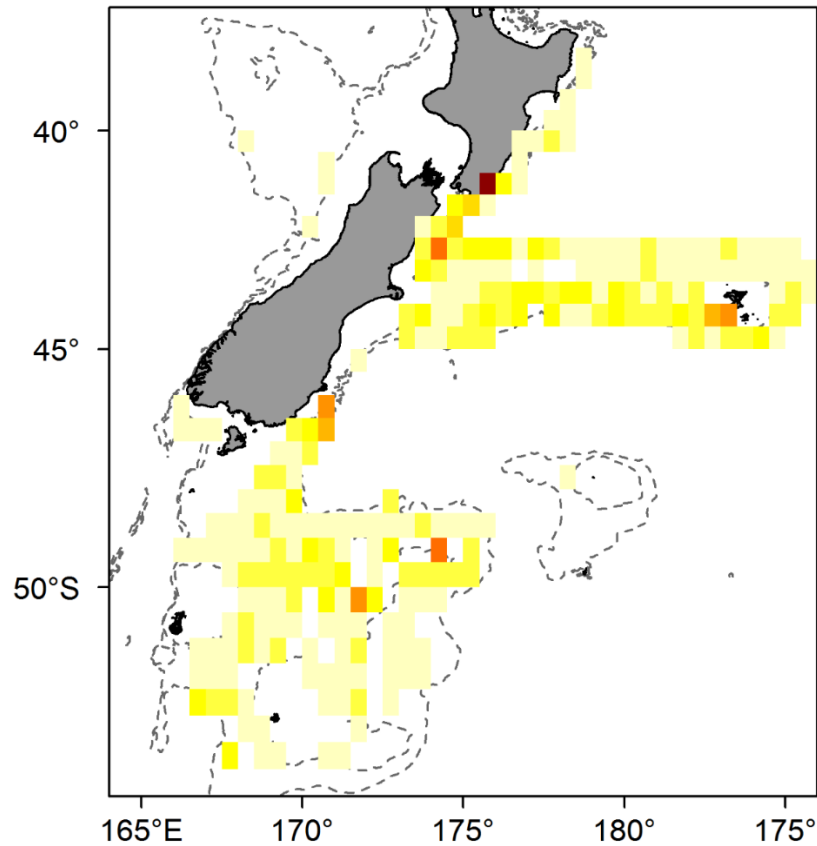
No tows met the criteria for a mating aggregation.

*Adult Habitat: Food Aggregation with Possible Mating*

We could not detect any food aggregation with possible mating (see Methods).

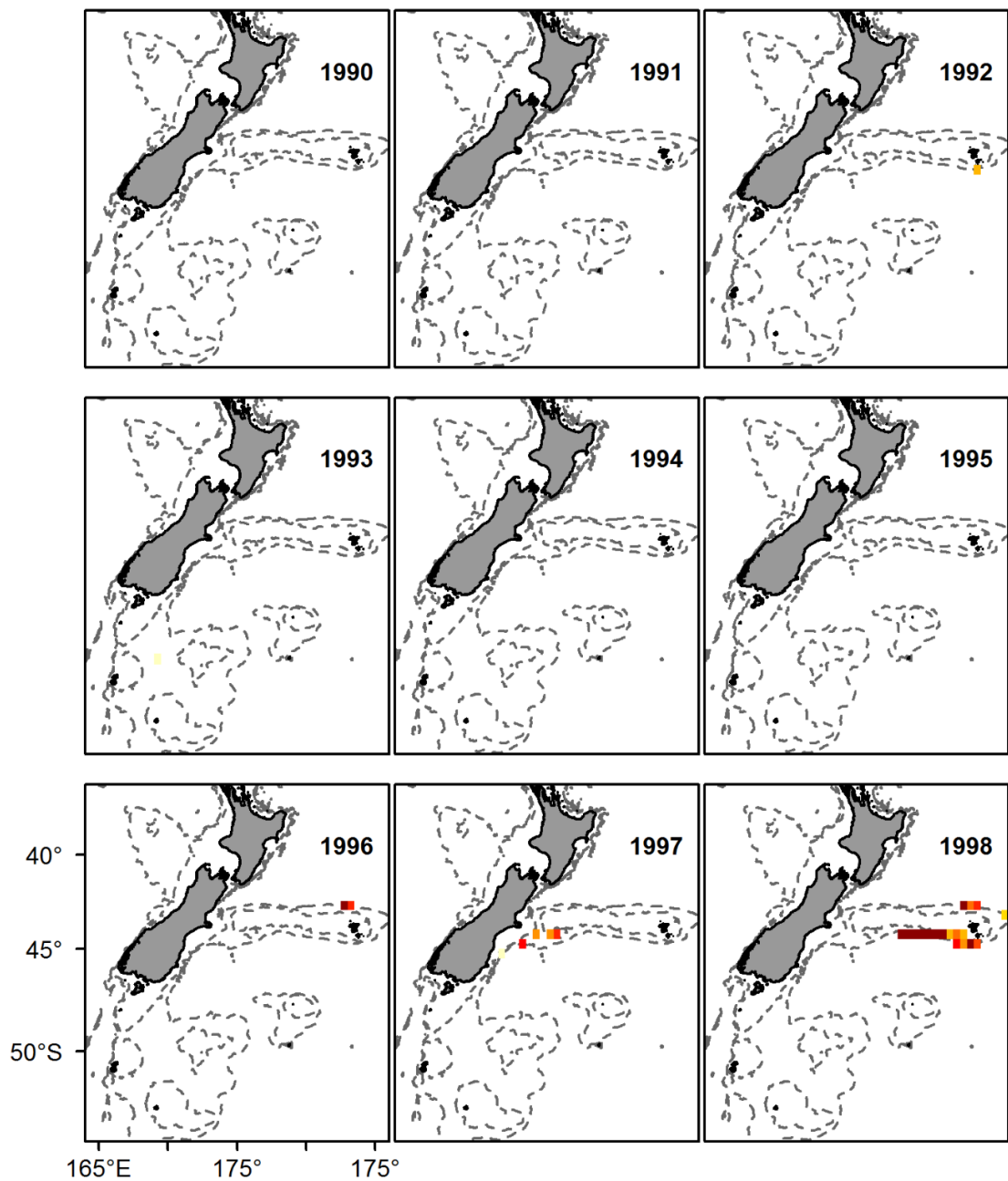
*Adult Habitat: Exclusive Foraging Ground*

We could not detect an exclusive foraging ground (see Methods).

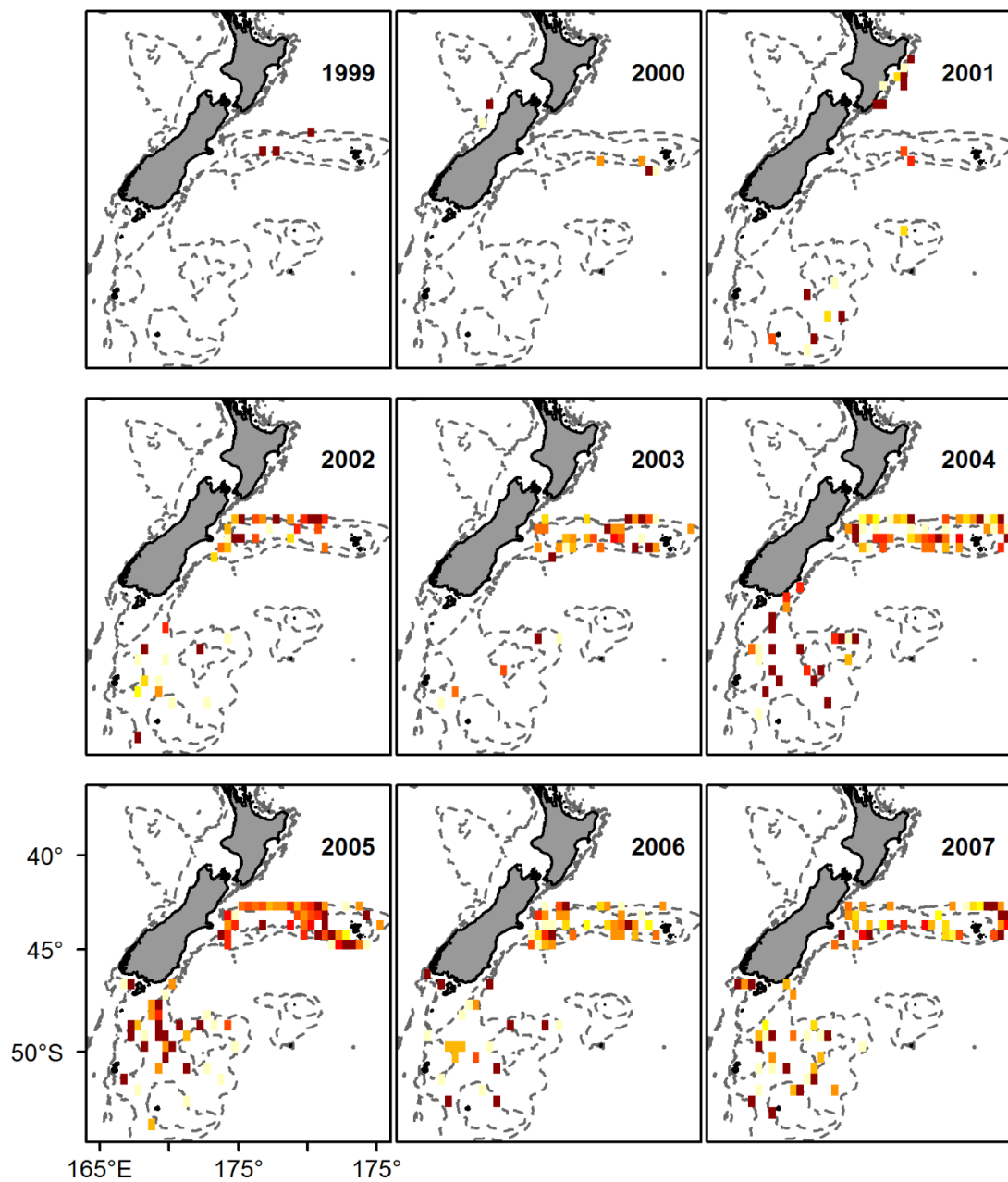


**Figure 42.** Relative distribution of female *Harriotta raleighana* from 1990-2014. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).

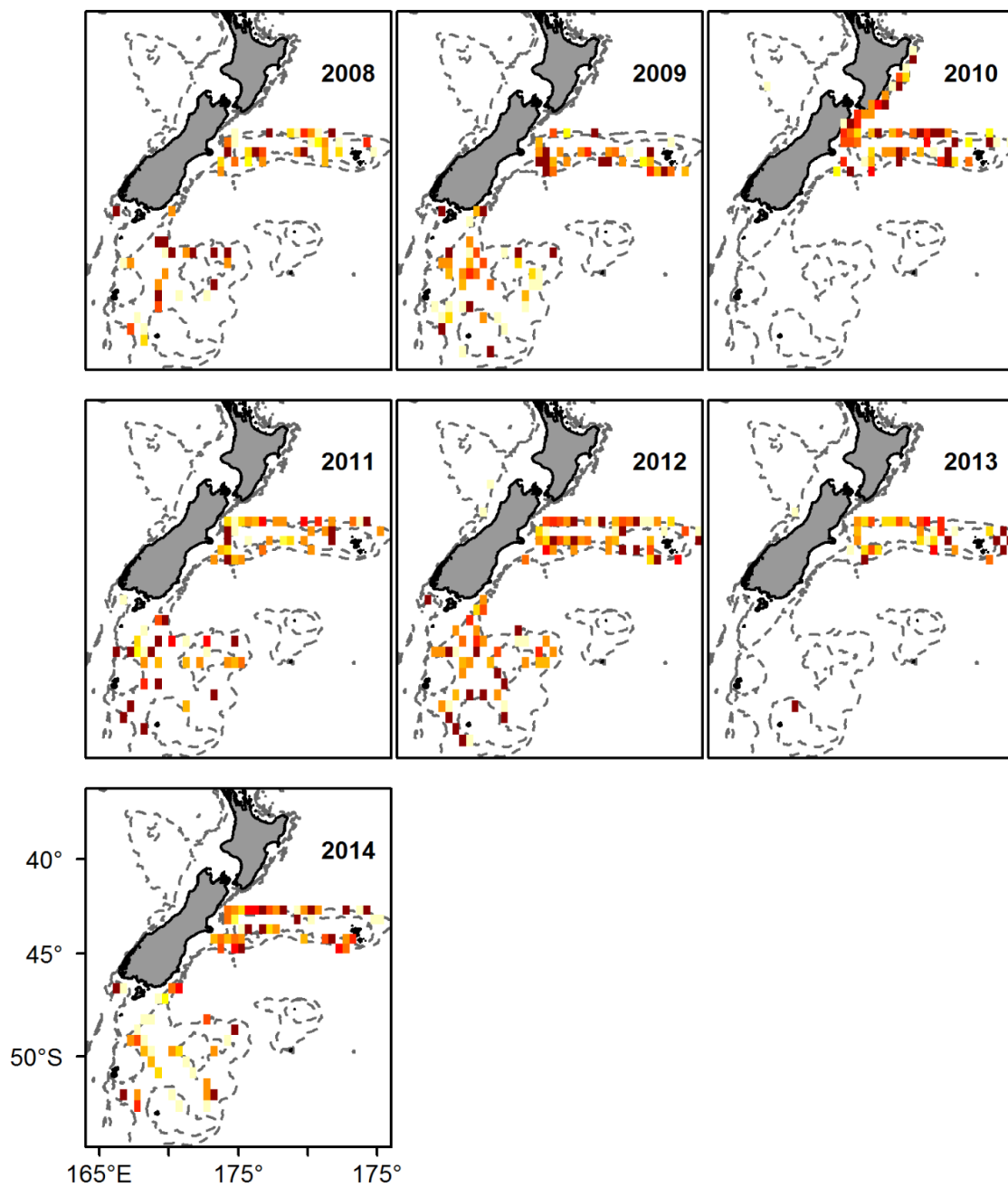
Records of female *Harriotta raleighana* distribution between 1990-2014 found relatively high numbers off of the South Island's Campbell Plateau shelf and Chatham Rise, and the North Island's Flat Point and along the Hikurangi Trough (**Fig 42**). North Island's Flat Point (dark red square) had high numbers of both females and males for 2001 and 2010. Year by year analysis showed the patchiness of the female *H. raleighana* occurrence (**Fig 43**). Of 1430 tows, 445 tows were female dominated.



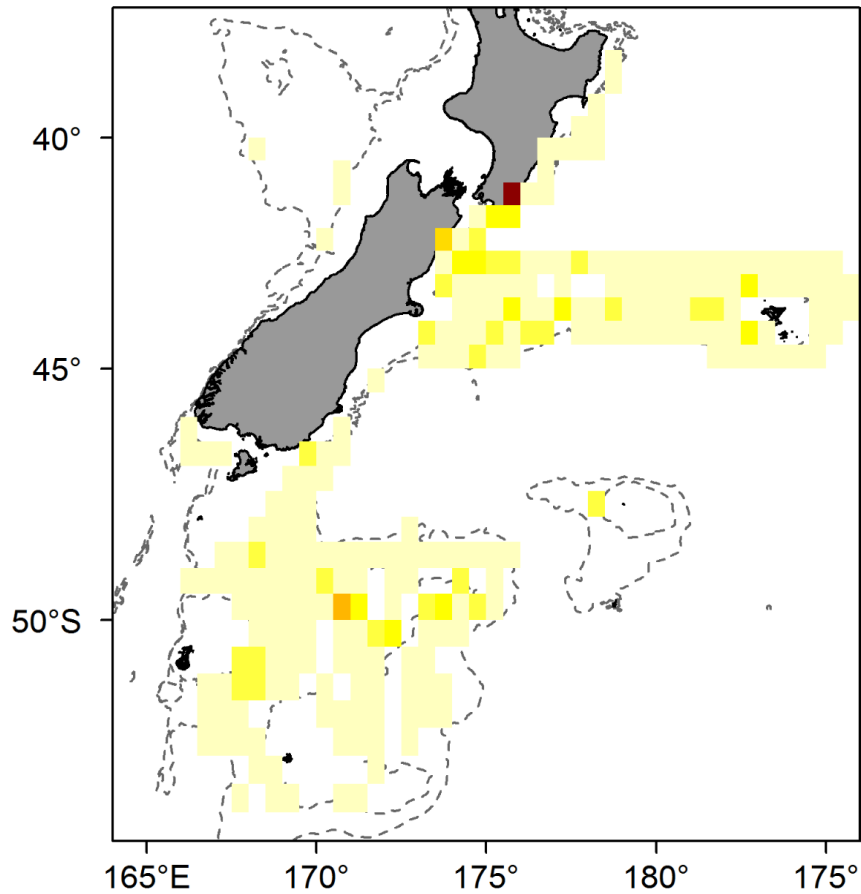
**Figure 43.** Relative distribution numbers of female *Harriotta raleighana* that were caught and measured in research survey trawls between 1990-1998. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).



**Figure 43 (cont).** Relative distribution numbers of female *Harriotta raleighana* that were caught and measured in research survey trawls between 1999-2007. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).

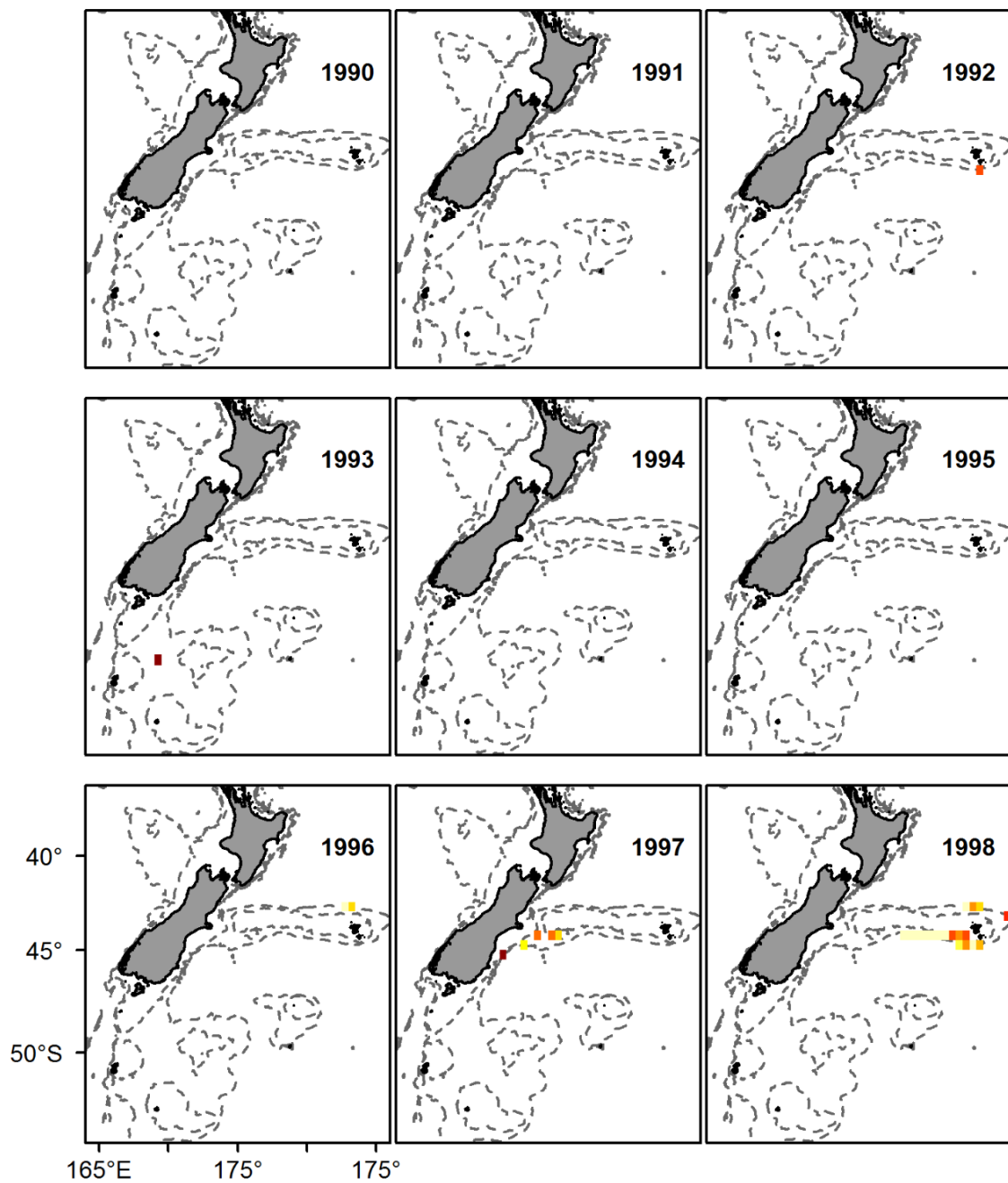


**Figure 43 (cont).** Relative distribution numbers of female *Harriotta raleighana* that were caught and measured in research survey trawls between 2008-2014. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).



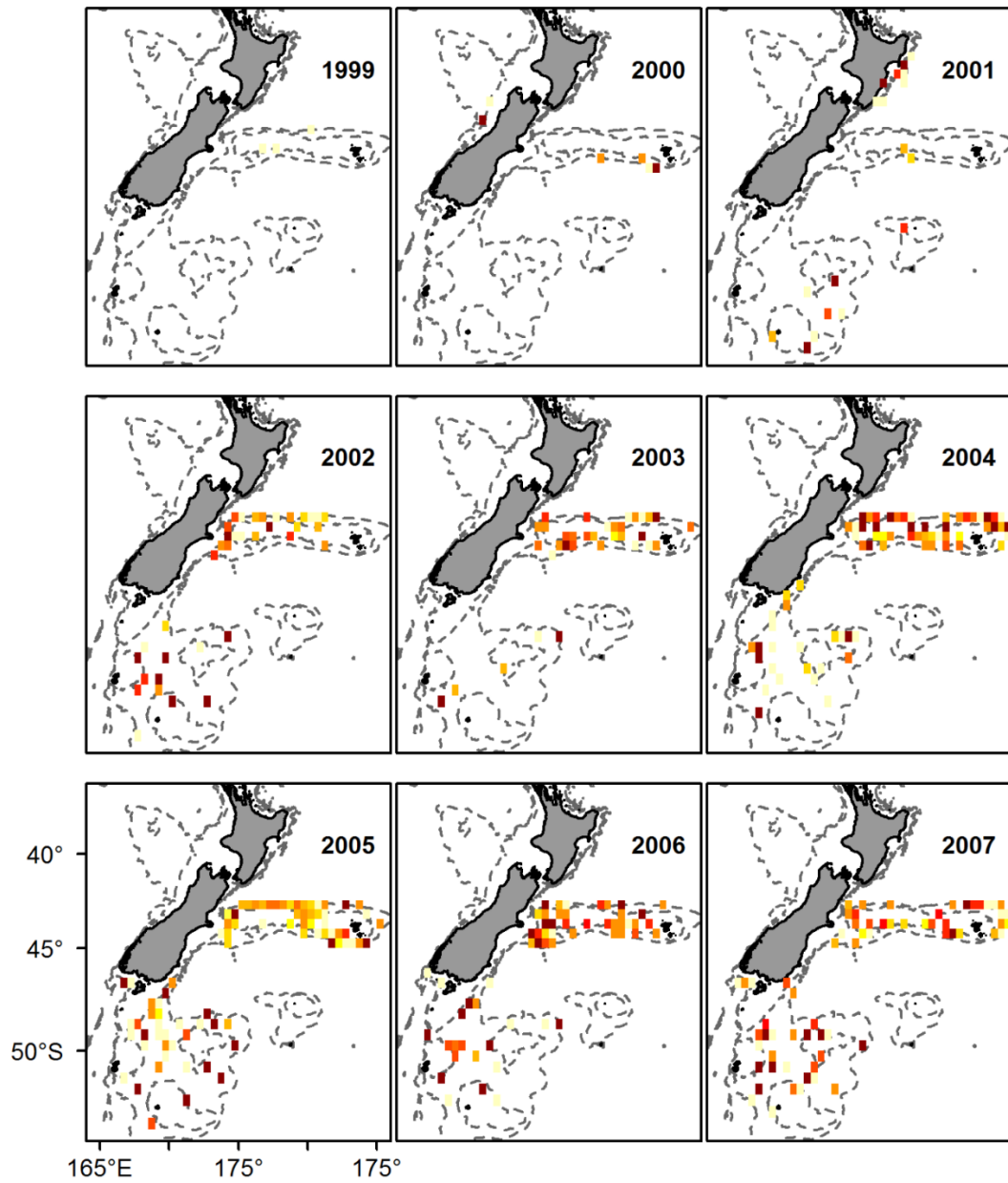
**Figure 44.** Relative distribution of number of male *Harriotta raleighana* that were caught and measured in research survey trawls between 1990-2014. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).

Records of male *Harriotta raleighana* distribution between 1990-2014 found relatively high numbers along the Chatham Rise and on the Campbell Plateau (**Fig 44**). North Island's Flat Point (dark red square) had high numbers of both males and females for 2001 and 2010. Year by year analysis (**Fig 45**) found high numbers of male *H. raleighana* being highly fragmented. Of 1430 tows, 843 tows were male dominated, but none met the criteria of a lek.

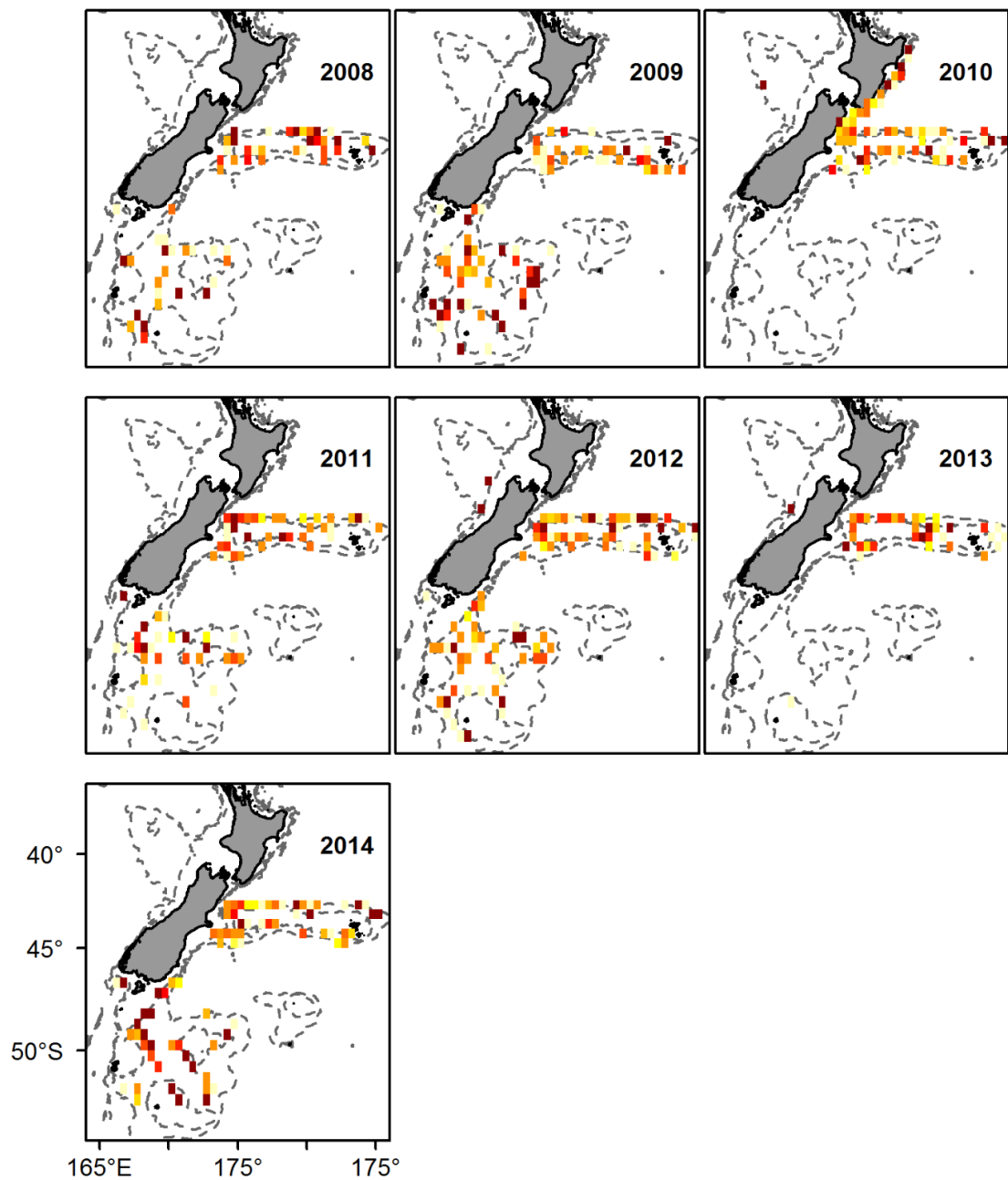


**Figure 45.** Relative distribution numbers of male *Harriotta raleighana* that were caught and measured in research survey trawls between 1990-1998. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).





**Figure 45 (cont).** Relative distribution numbers of male *Harriotta raleighana* that were caught and measured in research survey trawls between 1999-2007. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).



**Figure 45 (cont).** Relative distribution numbers of male *Harriotta raleighana* that were caught and measured in research survey trawls between 2008-2014. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).

### ***Harriotta raleighana* summary**

From 1990-2014, there was a total of 1430 tows that caught and measured *Harriotta raleighana*. Records were within (53.47° S, 35.99° S) and (166.2° E, 185.9° E) (**Fig 37**) with a depth range of 17-3678 meters, and an average of 731.7 meters (**Fig 38**).

Of the 4377 tows, the following tows were found which matched the criteria for:

1. Mating grounds (n=1218)

No tows were found that met the criteria for:

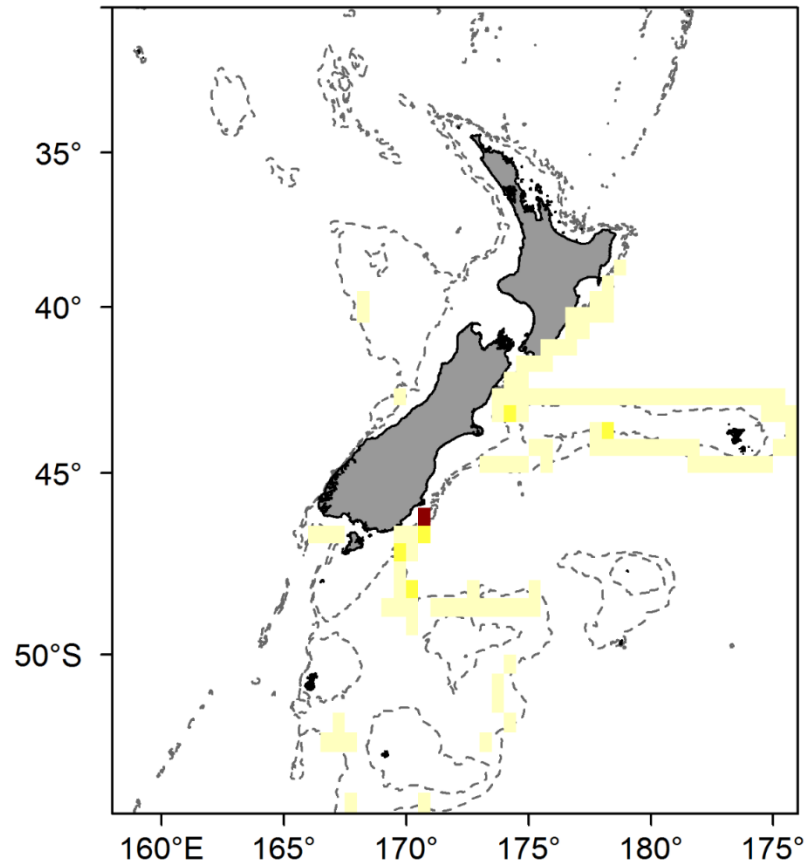
2. Pupping grounds
3. Nursery grounds
4. Leks

Whilst aggregations occurred, data were not available to distinguish:

5. Food aggregation with possible mating
6. Exclusive foraging grounds

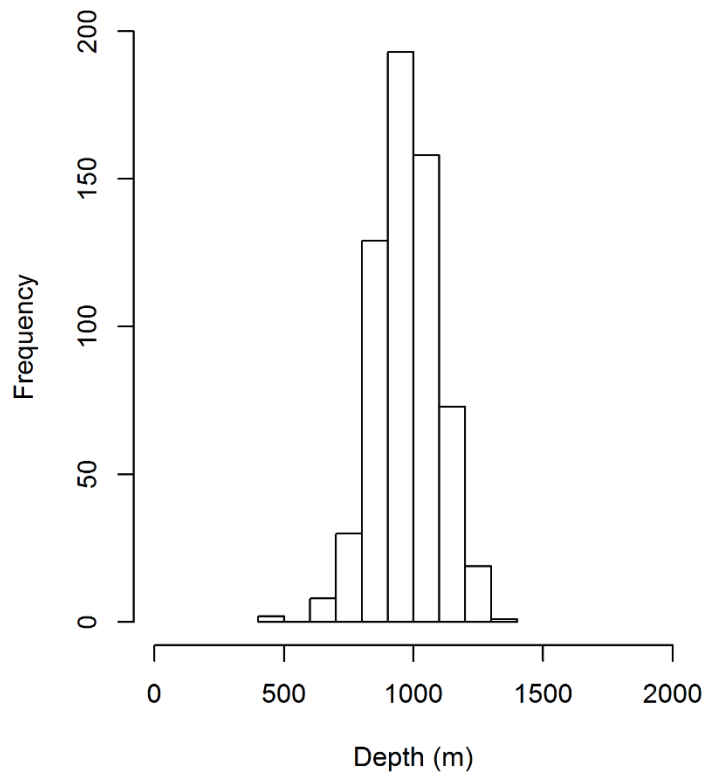
Adult and juvenile *H. raleighana* were caught along the Hikurangi Trough and along the outskirts of the Chatham Rise and on Campbell Plateau. Juveniles and adults seemed to share similar mean depths (714.7 m for juveniles and 656.5 m for adults), but adults extended into deeper water (888 m maximum depth for juveniles, 3678 maximum depth for adults). There were 843 tows that were female-dominated (mature and juvenile) and 445 tows that were male-dominated (mature and juvenile).

**Pacific Spookfish (Code: RCH; *Rhinochimaera pacifica*)**



**Figure 46.** Relative distribution of number of *Rhinochimaera pacifica* that were caught and measured in research survey trawls between 1990-2014. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).

From 1990-2014, there were a total of 613 tows where *Rhinochimaera pacifica* were caught and measured (**Fig 46**). Of these tows, 84% of *Rhinochimaera pacifica* were caught using gear code 1; 13.5% were caught using gear code 2. Records of *Rhinochimaera pacifica* were within the coordinates 53.68°S, 34.76°S – 166.2°E, 186.1°E from a minimum depth of 463 meters, maximum depth of 1306 meters, and a mean depth of 971.2 meters (**Fig 47**). Relatively high numbers of *Rhinochimaera pacifica* were caught off South Island's Invercargill (**Fig 46**), while low numbers of *Rhinochimaera pacifica* were caught on Challenger Plateau and Campbell Plateau and none were caught at the north of the North Island.



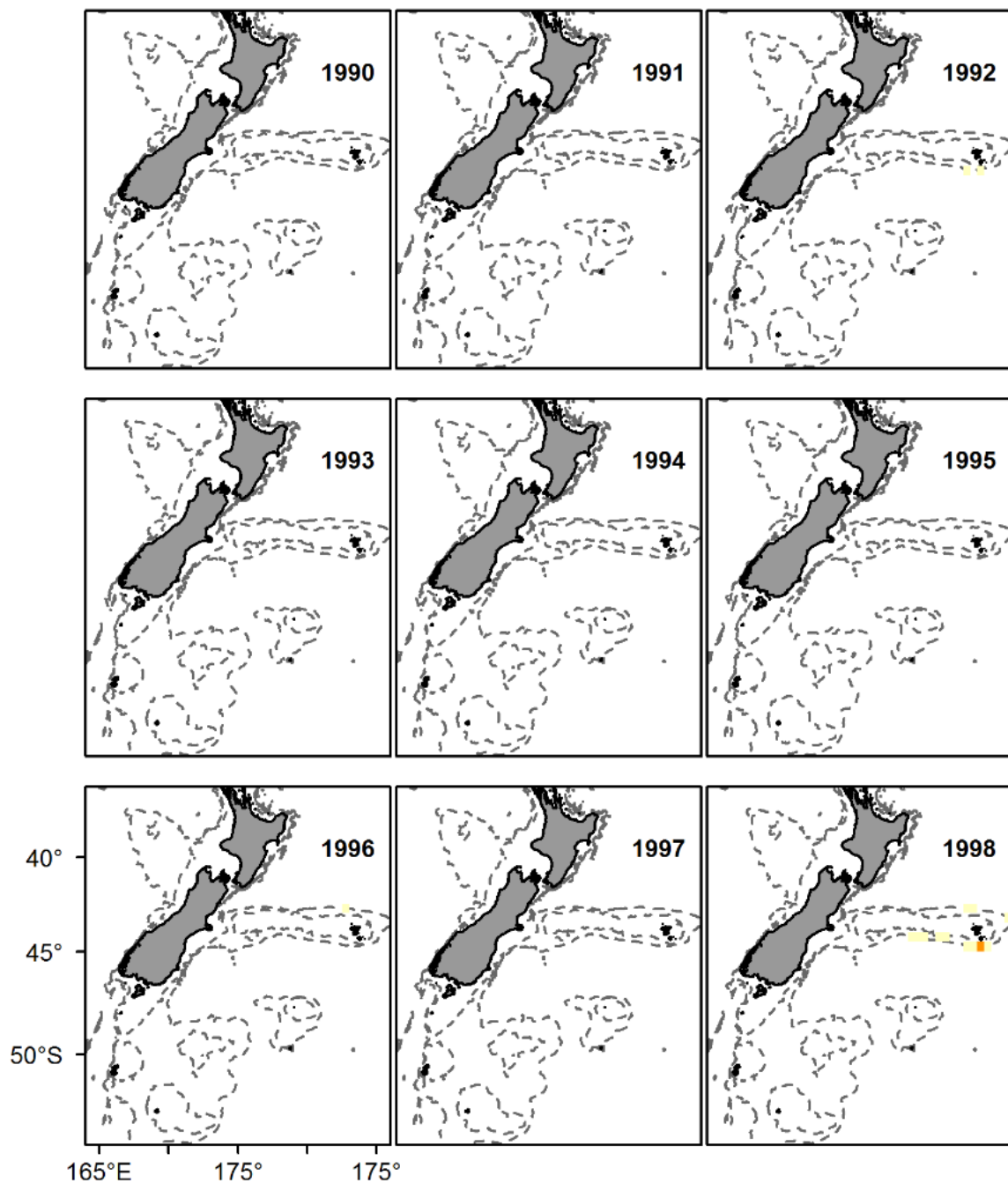
**Figure 47.** Relative frequency of catch records of *Rhinochimaera pacifica* by depth. Records from research survey trawls (n=613). Depth range of overall dataset (n= 34967) 0-8468 (mean =435.2).

#### *Habitat: Pupping Locations*

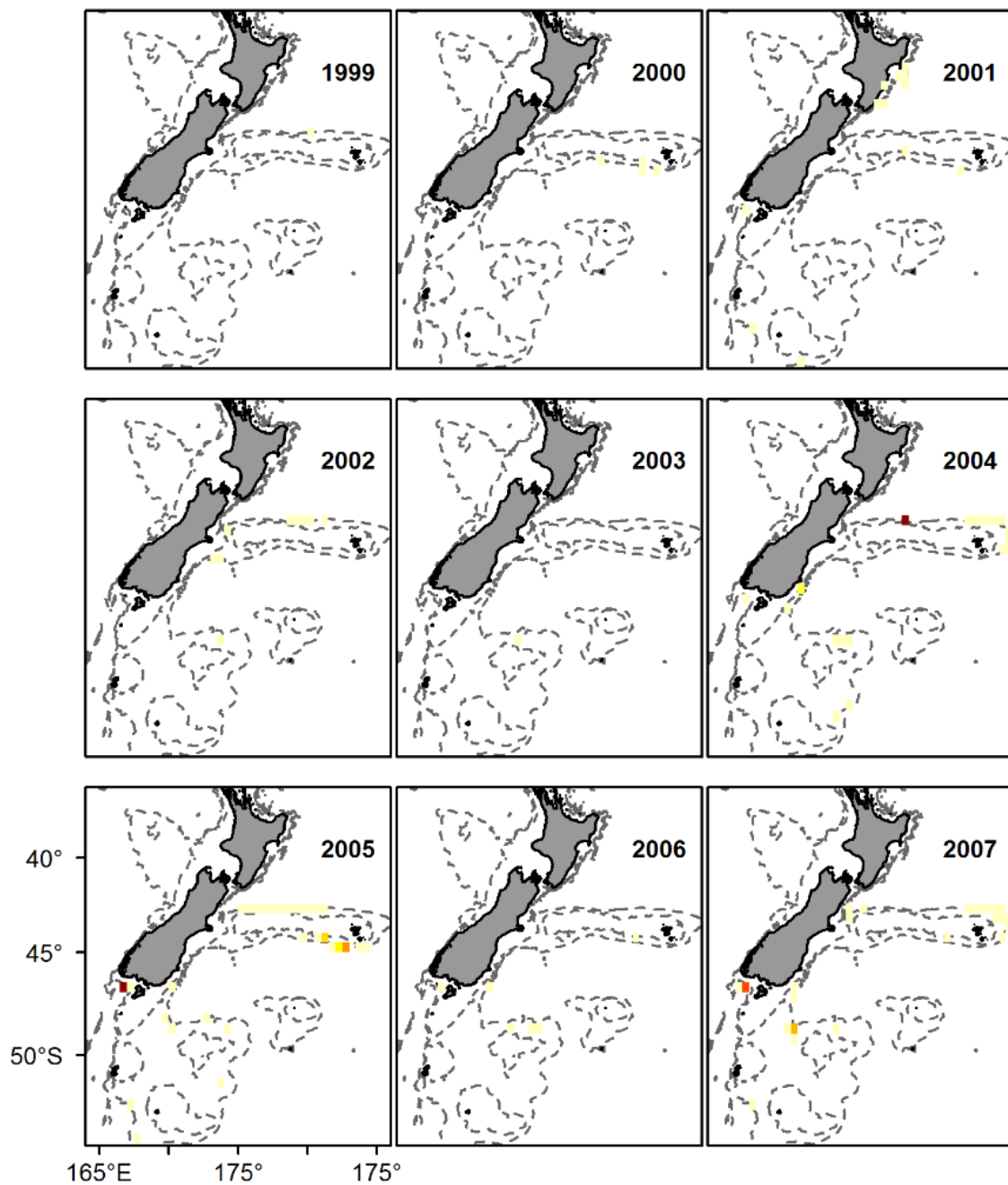
No tows met the criteria for a pupping location.

#### *Juvenile Habitat: Nurseries*

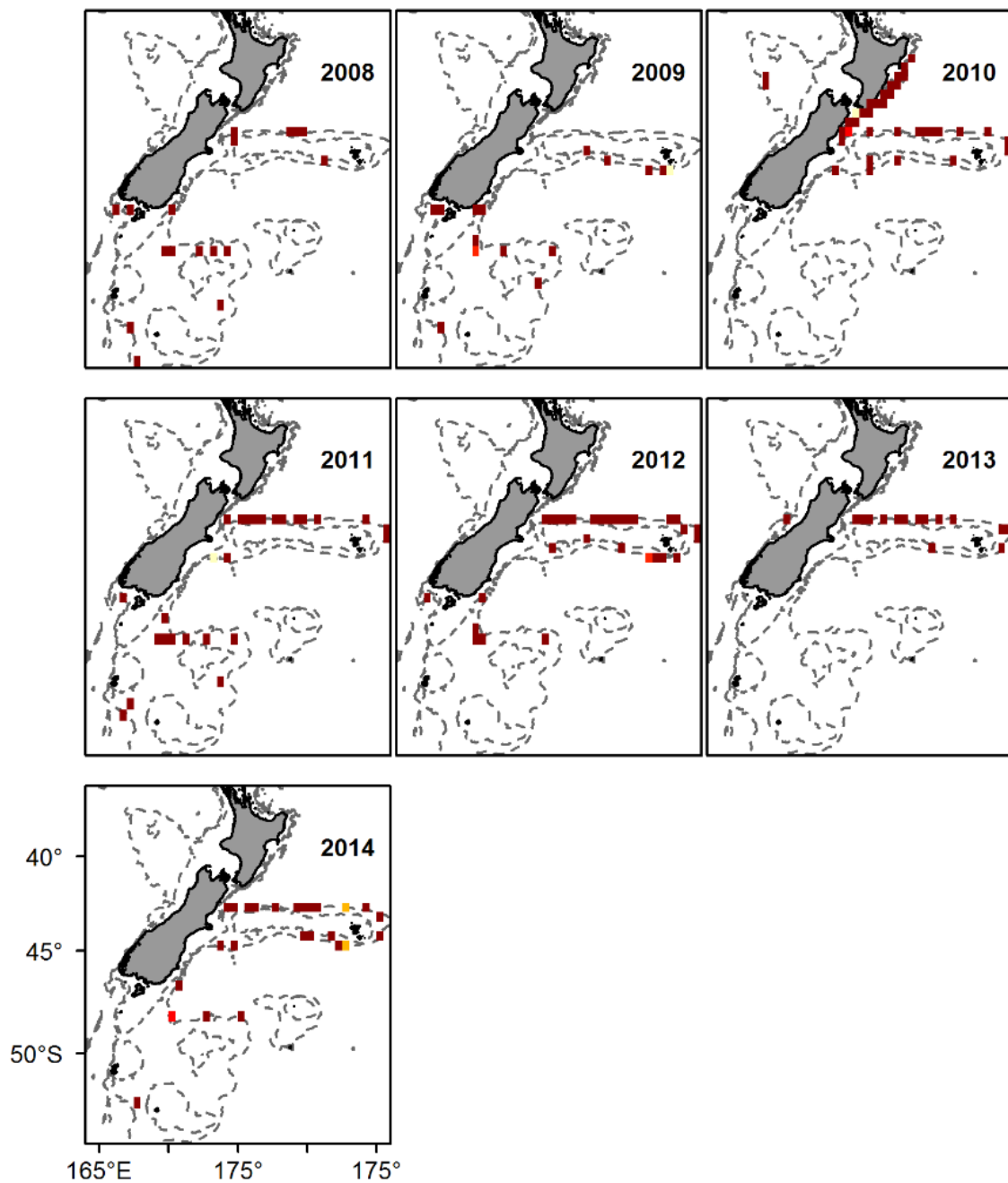
*Rhinochimaera pacifica* distribution found no tows which met the criteria for nursery grounds, although there were juveniles caught on the Campbell Plateau, along the Hikurangi Trough and on the Chatham Rise, especially near the Chatham Islands (**Fig 48**). Numbers seemed to increase after the year 2008. Other juvenile measurements (such as depth, coordinates, etc.) were unable to be obtained due to such low catch numbers.



**Figure 48.** Relative distribution numbers of juvenile *Rhinochimaera pacifica* that were caught and measured in research survey trawls between 1990-1998. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).

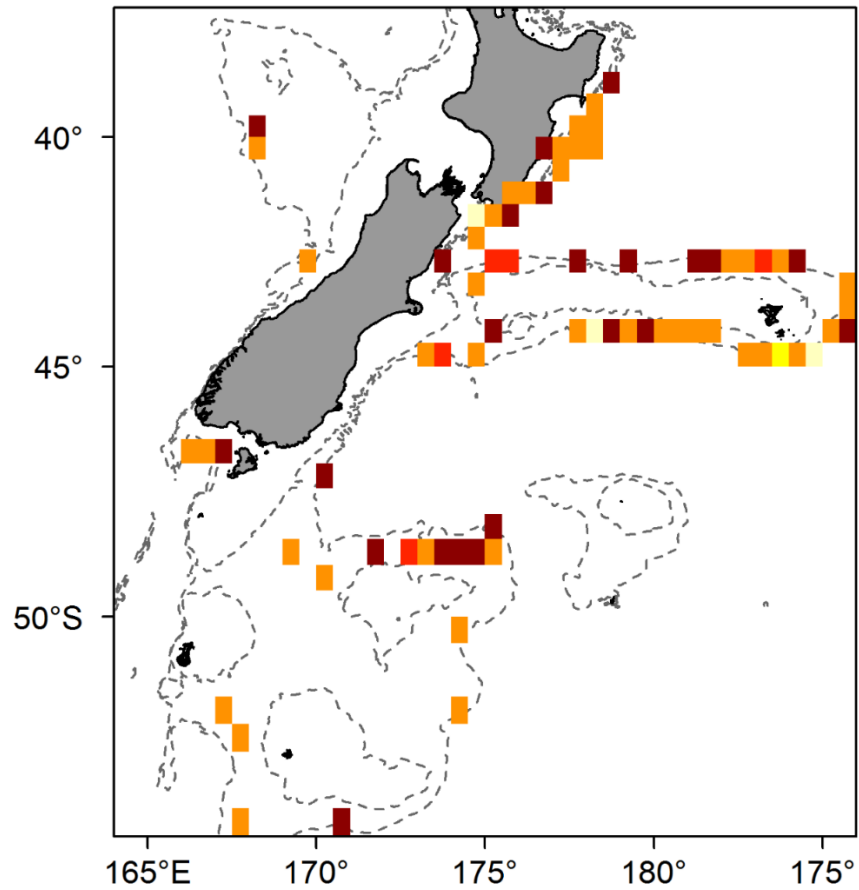


**Figure 48 (cont).** Relative distribution numbers of juvenile *Rhinochimaera pacifica* that were caught and measured in research survey trawls between 1999-2007. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).



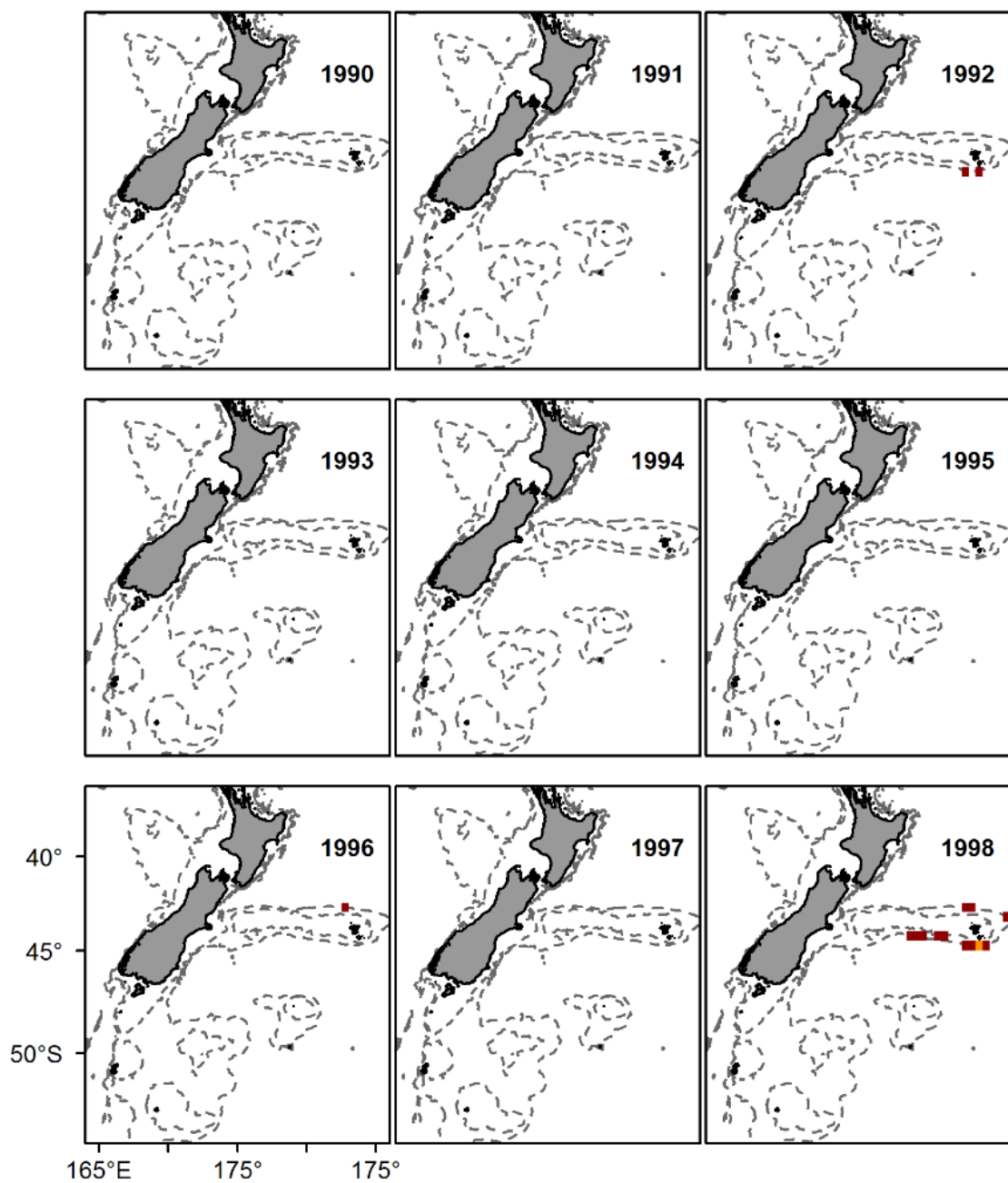
**Figure 48 (cont).** Relative distribution numbers of juvenile *Rhinobimaera pacifica* that were caught and measured in research survey trawls between 2008-2014. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).



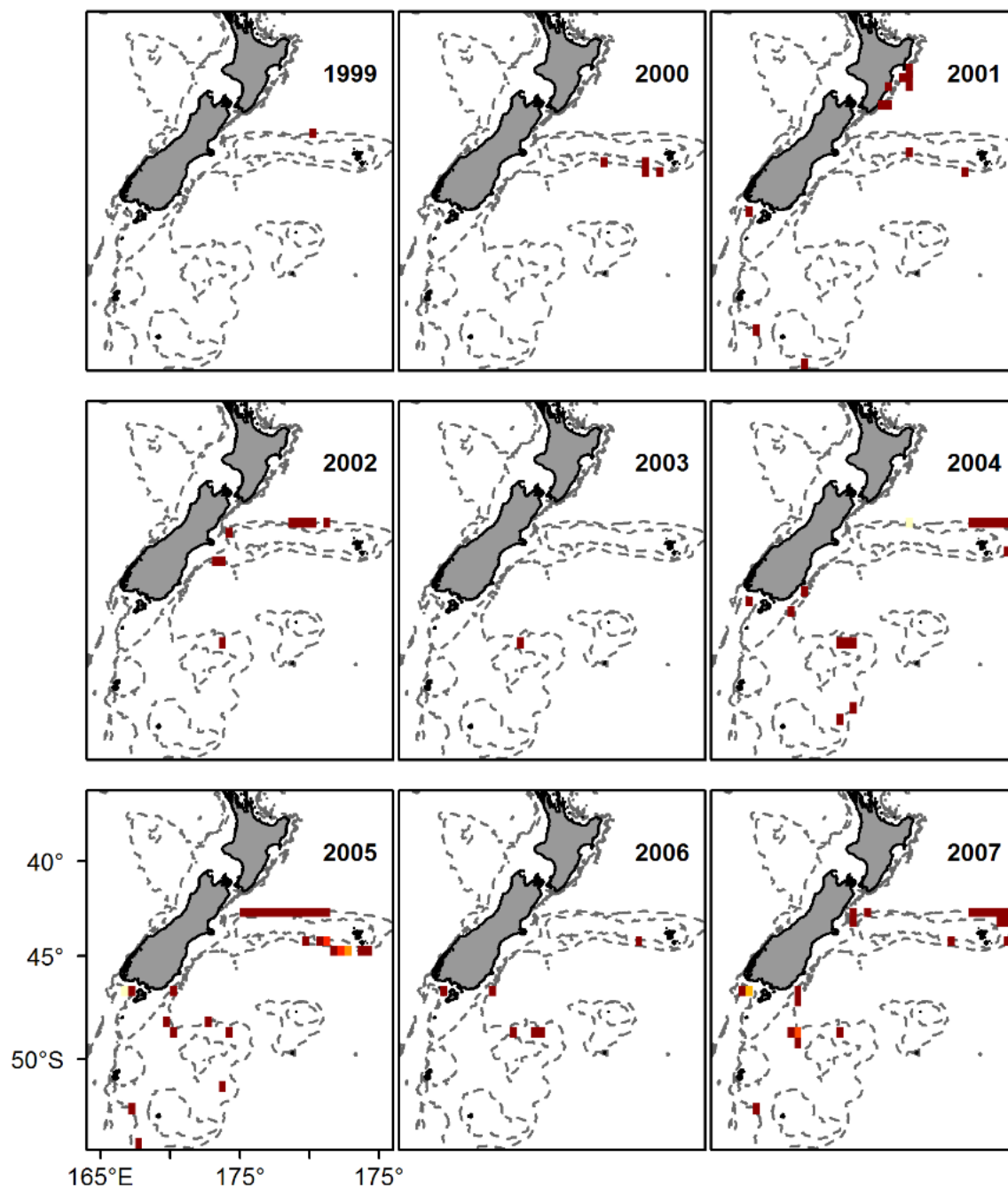


**Figure 49.** Relative distribution numbers of adult *Rhinochimaera pacifica* that were caught and measured in research survey trawls between 1990-2014. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).

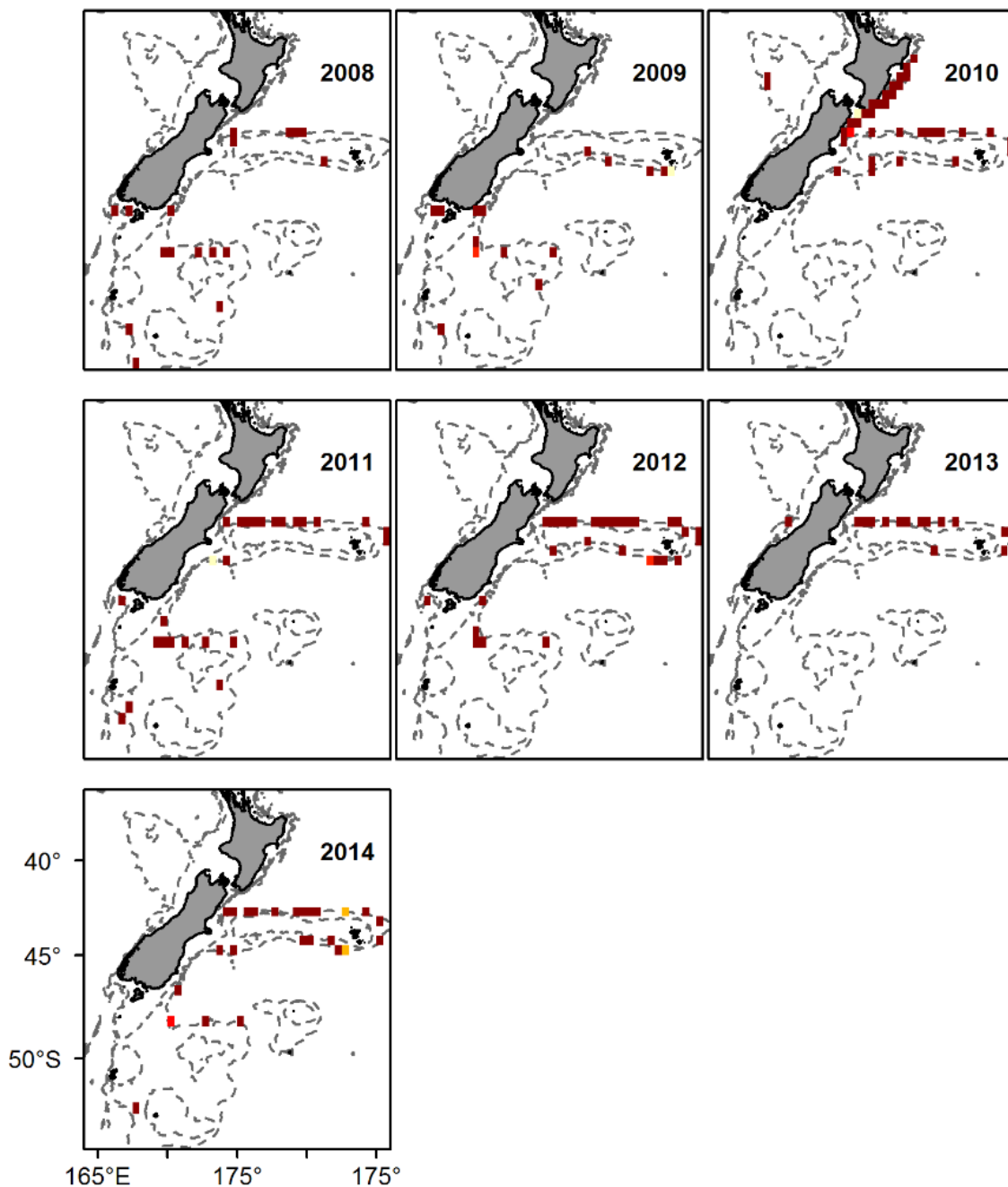
The overall distribution of adults (males and females) of *Rhinochimaera pacifica* between 1990-2014 found high densities off Stewart Island, the Chatham Islands on Chatham Rise and along the Hikurangi Trough (**Fig 49**). Year by year analysis found high numbers of adults on the Campbell Plateau (**Fig 50**).



**Figure 50.** Relative distribution numbers of adult *Rhinochimaera pacifica* that were caught and measured in research survey trawls between 1990-1998. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).



**Figure 50 (cont).** Relative distribution numbers of adult *Rhinochimaera pacifica* that were caught and measured in research survey trawls between 1999-2007. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).



**Figure 50 (cont).** Relative distribution numbers of adult *Rhinochimaera pacifica* that were caught and measured in research survey trawls between 2008-2014. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).

Average adult depth was 970.6 m with a minimum depth of 463 m and maximum depth of 1306 m. Adults were recorded between the coordinates 53.68° S, 34.76° S - 166.2° E, 186.1° E.

*Adult habitat: Mating Ground*

No tows met the criteria for a mating ground.

*Adult Habitat: Possible Mating Ground (Lek)*

No tows met the criteria for a lek.

*Adult Habitat: Possible Mating Ground (Aggregation)*

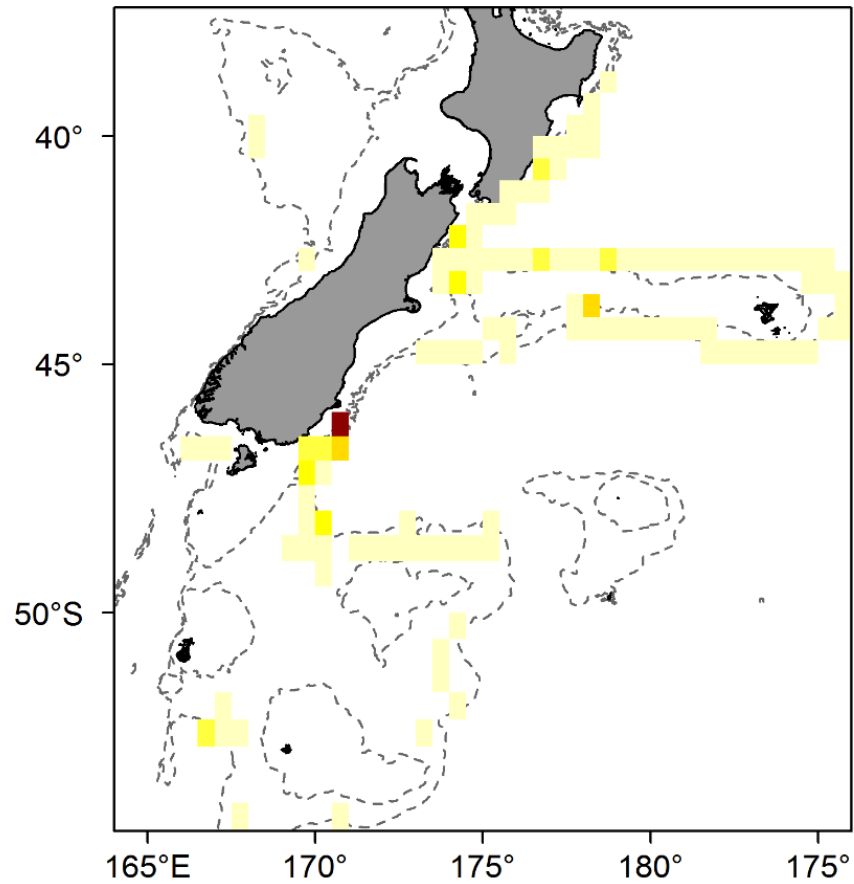
No tows met the criteria for a mating aggregation.

*Adult Habitat: Food Aggregation with Possible Mating*

We could not detect any food aggregation with possible mating (see Methods).

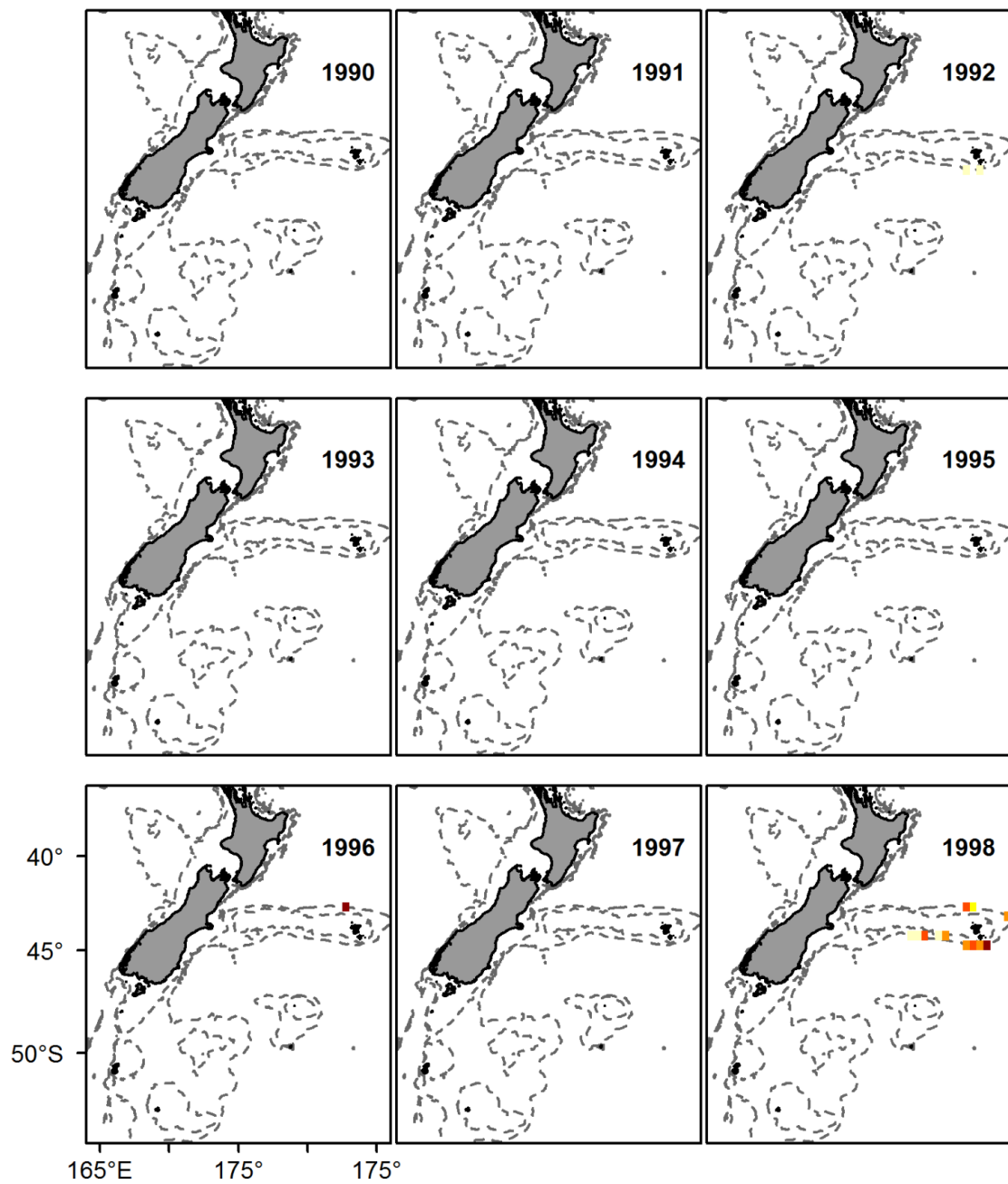
*Adult Habitat: Exclusive Foraging Ground*

We could not detect an exclusive foraging ground (see Methods).

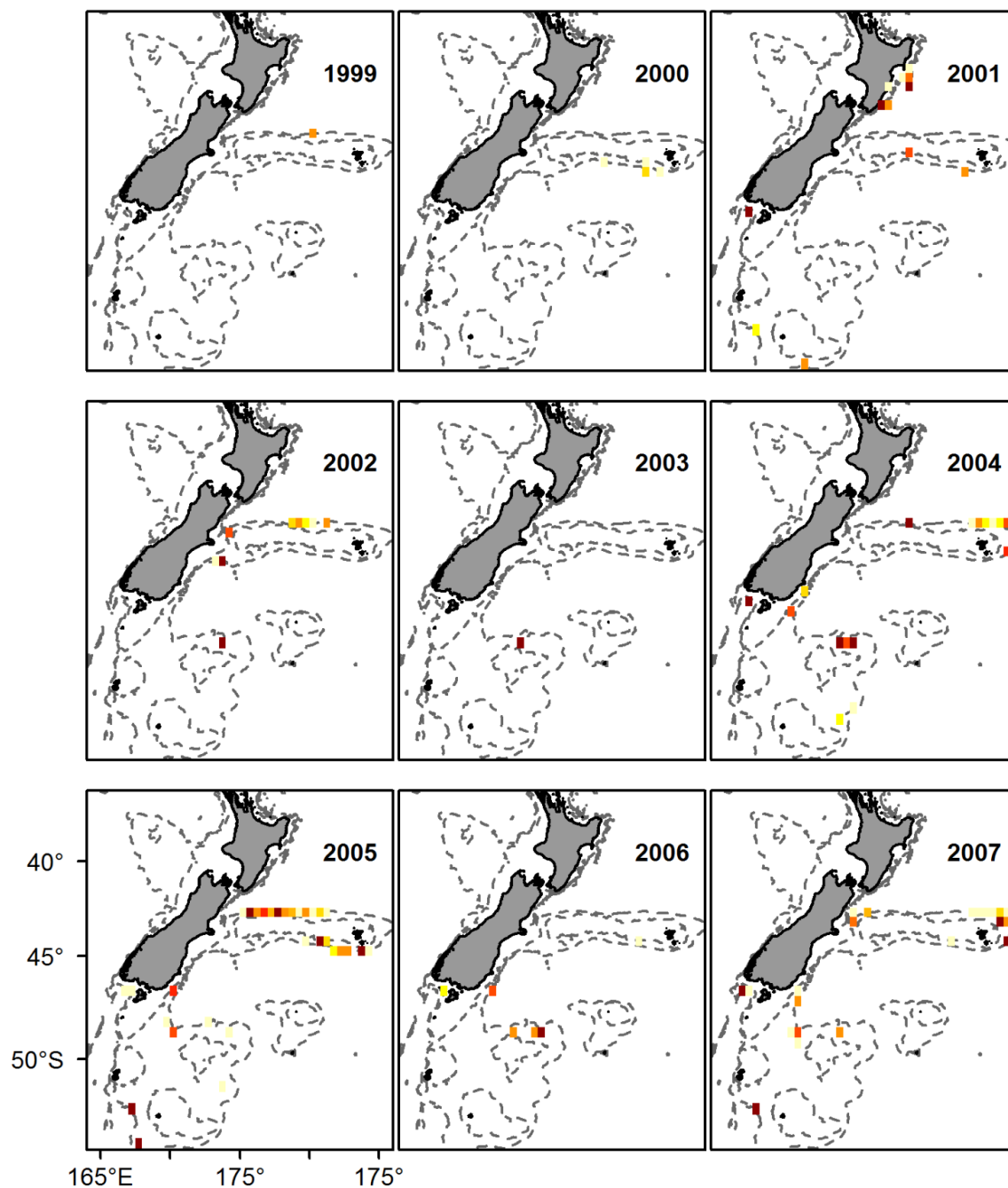


**Figure 51.** Relative distribution of female *Rhinochimaera pacifica* from 1990-2014. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).

Records of female *Rhinochimaera pacifica* distribution between 1990-2014 found relatively high numbers off of the South Island's Dunedin area, and low numbers on the Campbell Plateau and Chatham Rise and the Hikurangi Trough (**Fig 51**). Year by year analysis showed the patchiness of the female *Rhinochimaera pacifica* occurrence (**Fig 52**). Of 613 tows, 146 tows were female dominated.

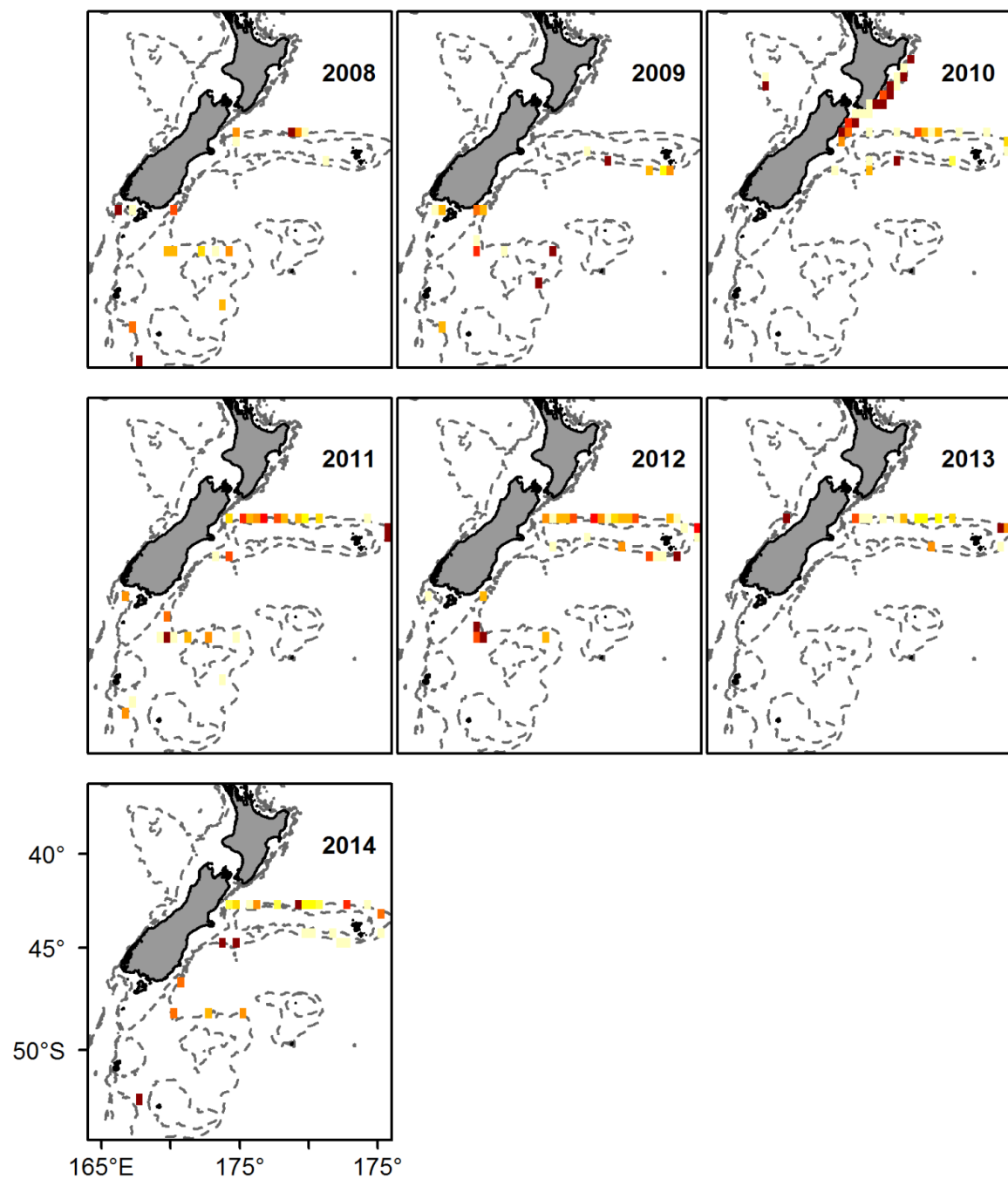


**Figure 52.** Relative distribution numbers of female *Rhinochimaera pacifica* that were caught and measured in research survey trawls between 1990-1998. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).

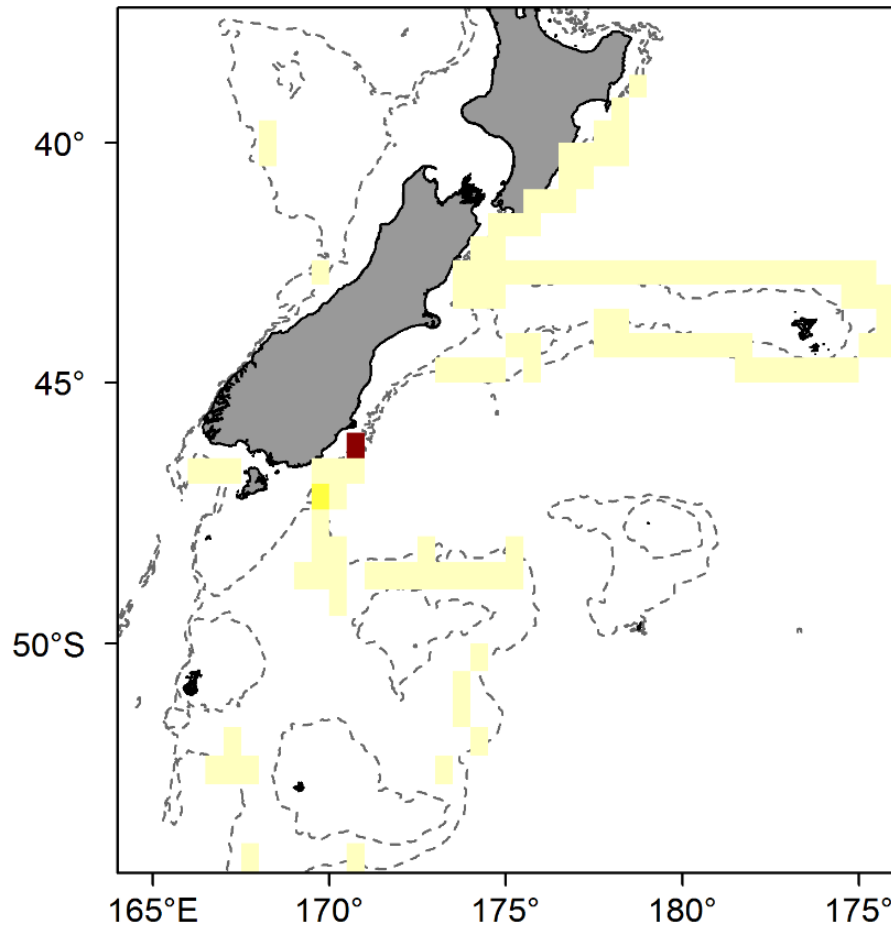


**Figure 52 (cont).** Relative distribution numbers of female *Rhinochimaera pacifica* that were caught and measured in research survey trawls between 1999-2007. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).



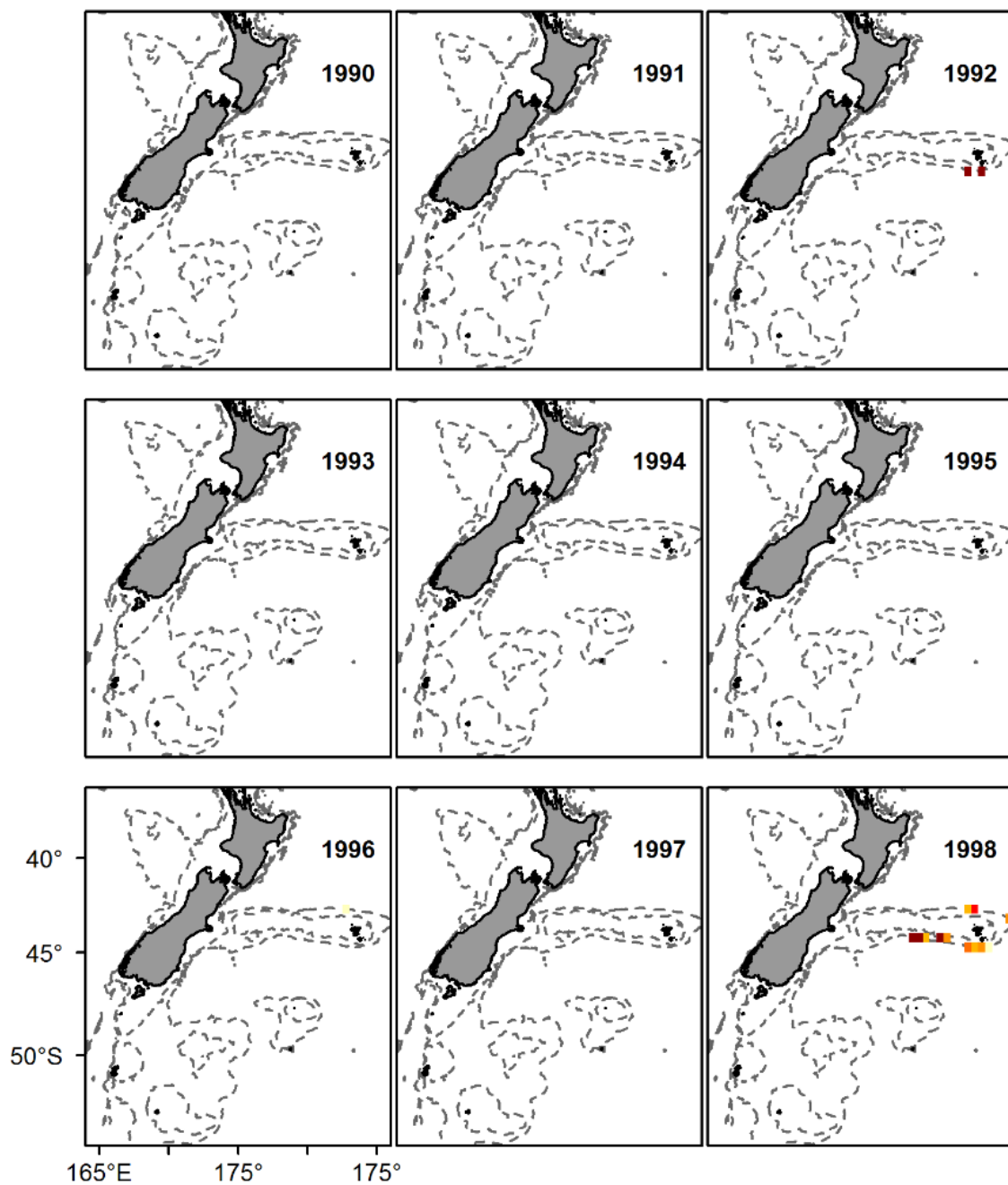


**Figure 52 (cont).** Relative distribution numbers of female *Rhinochimaera pacifica* that were caught and measured in research survey trawls between 2008-2014. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).

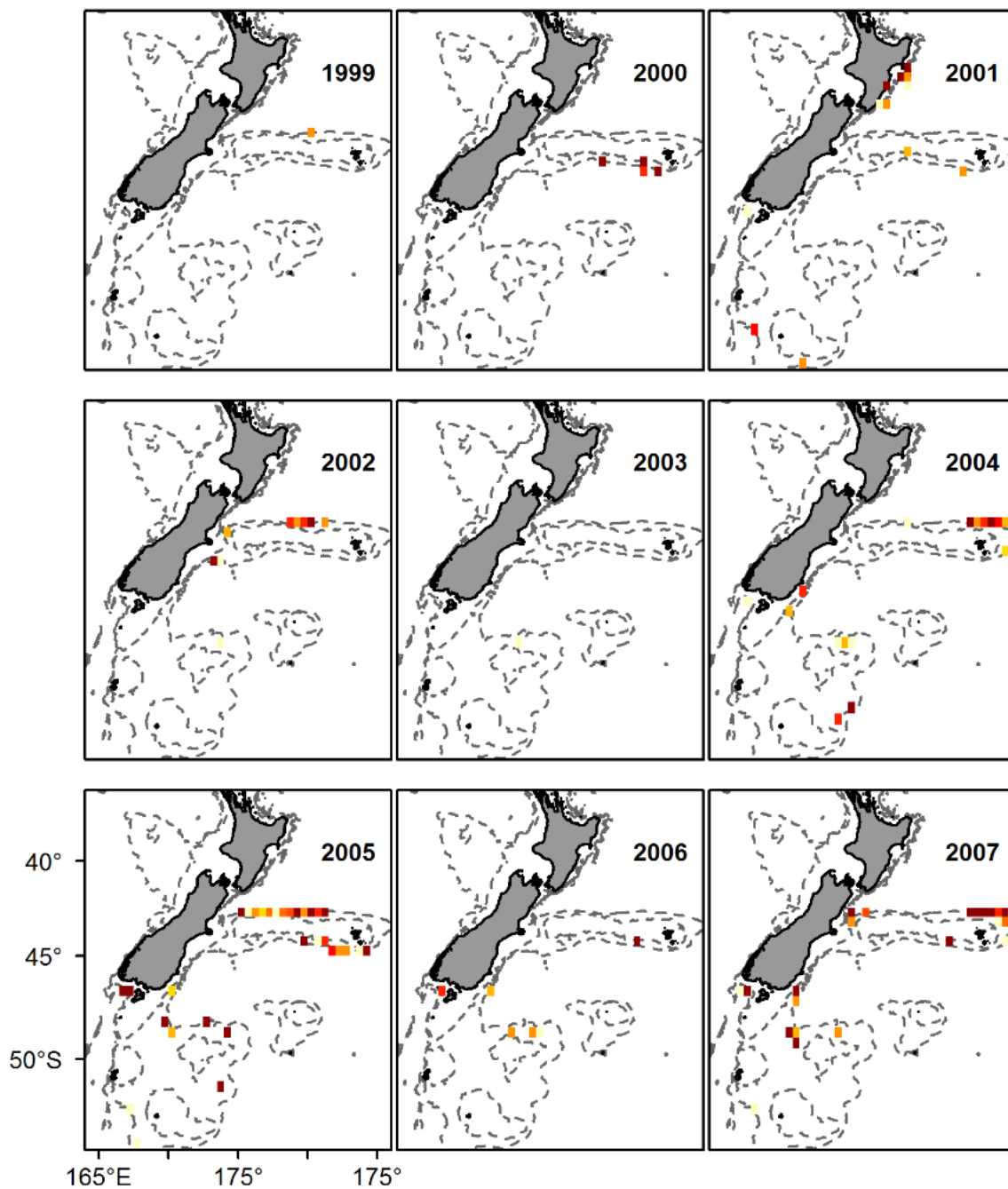


**Figure 53.** Relative distribution of number of male *Rhinochimaera pacifica* that were caught and measured in research survey trawls between 1990-2014. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).

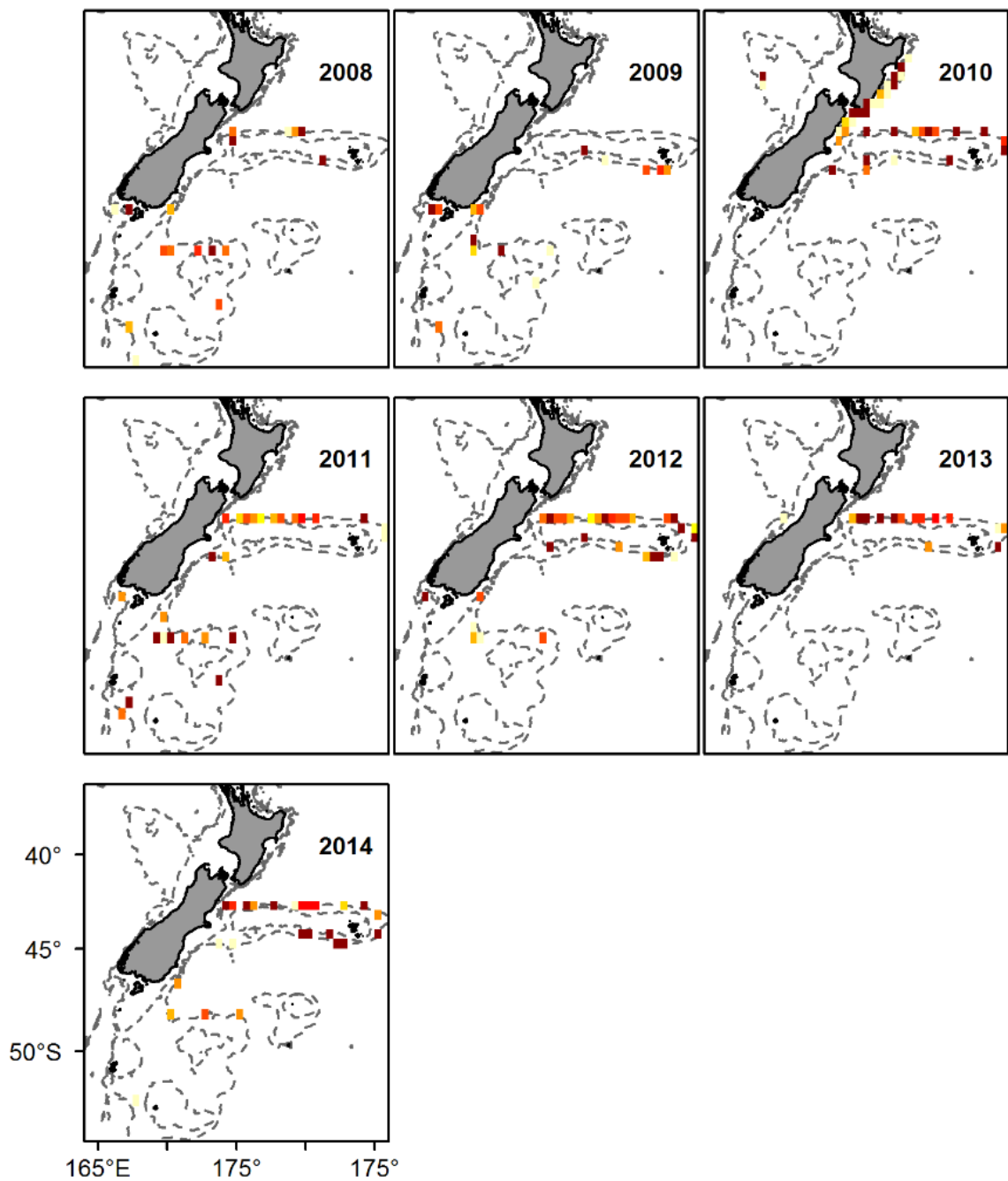
Records of male *Rhinochimaera pacifica* distribution between 1990-2014 found relatively high numbers off South Island's Dunedin, and low numbers along the Chatham Rise and on the Campbell Plateau (**Fig 53**). Year by year analysis (**Fig 54**) found high numbers of male *R. pacifica* being highly fragmented. Of 613 tows, 440 tows were male dominated, but none met the criteria of a lek.



**Figure 54.** Relative distribution numbers of male *Rhinochimaera pacifica* that were caught and measured in research survey trawls between 1990-1998. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).



**Figure 54 (cont).** Relative distribution numbers of male *Rhinochimaera pacifica* that were caught and measured in research survey trawls between 1999-2007. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).



**Figure 54 (cont).** Relative distribution numbers of male *Rhinochimaera pacifica* that were caught and measured in research survey trawls between 2008-2014. Density indicated by color, from light yellow (lowest), through orange, to dark red (highest).

### ***Rhinochimaera pacifica* summary**

From 1990-2014, there was a total of 613 tows that caught and measured *Rhinochimaera pacifica*. Records were within (53.68° S, 34.76° S) and (166.2° E, 186.1° E) (**Fig 46**) with a depth range of 463-1306 meters, and an average of 971.2 meters (**Fig 47**).

Of the 4377 tows, no tows were found that met the criteria for:

1. Pupping grounds
2. Nursery grounds
3. Mating grounds
4. Leks

Whilst aggregations occurred, data were not available to distinguish:

5. Food aggregation with possible mating
6. Exclusive foraging grounds

Adult and juvenile *R. pacifica* were caught along the Hikurangi Trough and along the outskirts of the Chatham Rise and on Campbell Plateau. There were 146 tows that were female-dominated (mature and juvenile) and 440 tows that were male-dominated (mature and juvenile).

## CHAPTER 3: DISCUSSION

In this thesis, I synthesized information (from 300+ literature articles) on habitat use by Chondrichthyans to develop hypotheses and criteria for habitat use. While locations falling under our habitat composition criteria for *Callorhynchus milii* (ELE), *Hydrolagus novaezealandiae* (GSH), *Hydrolagus bemisi* (GSP), *Harriotta raleighana* (LCH) and *Rhinochimaera pacifica* (RCH) were relatively rarely found (made up a small proportion of tows where they were caught), they are nevertheless areas to focus on (Table 9).

**Table 9.** A summary of results from the five species analysed: *Callorhynchus milii* (ELE), *Hydrolagus novaezealandiae* (GSH), *Hydrolagus bemisi* (GSP), *Harriotta raleighana* (LCH) and *Rhinochimaera pacifica* (RCH). Columns with N/A cannot be distinguished without detailed stomach content and reproductive data (see Methods).

CODE	PUPPING	NURSERY	MATING GROUND	MATING: LEK	MATING: AGG.	FOOD AGG. W/MATING	EXCLUSIVE FORAGING GROUND	FEMALE DOM TOWS	MALE DOM TOWS
ELE	4	10	2	0	N/A	N/A	N/A	245	410
GSH	14	0	195	45	N/A	N/A	N/A	484	1249
GSP	12	0	3906	0	N/A	N/A	N/A	820	3231
LCH	0	0	1218	0	N/A	N/A	N/A	445	843
RCH	0	0	0	0	N/A	N/A	N/A	146	440

Despite excellence progress made over the last century, our understanding of the distribution, origin, and evolution of the fishes in New Zealand is still in its early stages. It can be expanded by undertaking further surveys whose study objectives should be expanding biological data such as sampling stomach content (prey type, how full the stomach is, prey freshness) and reproductive status (mating scars, hardness of claspers, presence of sperm in spermatid ducts, ripe oocytes) (O'Driscoll et al. 2011).

The data suggested large geographical ranges for most species, with extensive overlap between juveniles and adults in some, and no persistent spatial sex segregation. No clear specific life-history stage related grounds were found (except for possible pupping grounds), leading to the hypotheses that either (1) they have not been found yet, and therefore are probably relatively safe as they are not

within the main fishing footprint, or (2) there is no discrete area or habitat associated with these life history stages, and they can occur everywhere. Species with no discrete pupping and nursery grounds may be at lower risk from fishing, because the fishing impact is diluted, whereas those with pupping grounds within the footprint of the hoki fishery (GSH, GSP) would be at higher risk. Pupping grounds of ELE are relatively safe due to safeguards (no fishing zones) put in place for Hector and Māui dolphin protection (Ministry for Primary Industries 2016).

### 3.1 JUVENILE HABITATS

#### Pupping Grounds

No one has discovered specific egg-laying locations for any deep-sea Chondrichthyans here in New Zealand. However, it is known that eggs are laid on sand or mud bottoms (Able and Flescher, 1991; Ellis and Shackley, 1997; Etnoyer and Warrenchuk, 2007; Love et al. 2008; Hoff 2010; Treude et al. 2011; Henry et al. 2016); depth of these locations vary by species. Further research into benthic imagery with a specific aim to look for Chondrichthyan eggs is suggested.

While research trawl surveys and other techniques have recognized where juveniles occur for many fisheries species, they are limited to where, when and what they can sample. Qualitative research with quantitative in-depth descriptions of these areas in relation to the importance for these species has never been pursued. Better collaboration with other scientists and programs could lead to a better understanding of habitat preference and use (e.g. multibeam bathymetry and Baited Remote Underwater Video Stations or BRUVS). This can eventually lead to important seafloor habitat mapping and related dynamic processes, especially of those rougher topographical areas and habitats in water depths <10 meters excluded from fisheries.

Trawl surveys, like those in New Zealand, have constraints around timing of voyages and different types of gear. Most gear is designed for catching adults and monitoring adult biomass of stocks, meaning juveniles could be missed during particular seasons in specific habitats. We found potential pupping grounds for *Callorhynchus milii* (n=4), *Hydrolagus novaezealandiae* (n=14), and *Hydrolagus bemisi* (n=12). We cannot say for certain these locations are pupping grounds without repeated observation over the course of many years, but it is interesting to note that the shallower chimaeras seem to have pupping grounds while deeper chimaeras (*Harriotta raleighana* and *Rhinochimaera pacifica*) do not.



Dedicated surveys to find and quantify juvenile grounds (i.e. pupping grounds and nurseries) are the solution to this problem, though standard trawl surveys may not be the best sampling approach (fishing is not representative of whole population).

### **Nursery: Inshore and Offshore**

Multiple Chondrichthyan species can occasionally use the same nursery area, but temporal or spatial separation of species is possible (e.g., Castro 1993; Simpfendorfer and Milward 1993). The coastal waters of New Zealand appear to be used as nursery grounds by juveniles of several elasmobranchs including two small sharks (rig, *Mustelus lenticulatus*; school shark, *Galeorhinus galeus*), three rays (long-tailed stingray, *Dasyatis thetidis*; short-tailed stingray, *D. brevicaudata*; eagle ray, *Myliobatis tenuicaudatus*), and a chimaeroid (elephantfish, *Callorhynchus milii*). For many species, however, we still do not know the location of nursery areas or whether young even inhabit distinct nurseries (Branstetter 1990).

Of roughly 10,000 tows, only ten tows fitted the criteria of a nursery. Tows of particular interest (10 locations) were identified from the trawl database for the shallowest of the chimaeras, *Callorhynchus milii* (ELE), as potential nursery grounds. The locations were less than 30 meters deep, in coastal waters (see water region definitions on page 41) and can be labeled as an inshore nursery. Shallow coastal waters are widely believed to be lower risk habitats due to shallower waters limiting access to large sharks, the primary predators of young sharks (e.g., Cliff et al. 1989; Cliff and Dudley 1991; Cliff 1995; Ebert 2002; Heithaus 2004). What benefits these ten locations (in similar coordinates) offer is still unknown, although these shallow areas (4 nautical miles offshore of the east coast of the South Island) are now closed for Hector and Māui dolphin protection (Ministry for Primary Industries 2016).

Offshore nursery areas were not found for any species, and the benefits that open water nursery areas provide are still unclear. However, juvenile Chondrichthyans in offshore nursery grounds could reduce predation risk by schooling (Branstetter 1990), or be dispersed in low densities over large areas. While observational field studies have provided strong support for predation risk as an important determination factor in regards to choice of a nursery area (e.g. Heupel and Hueter, 2002), other determining factors are unclear due to lack of experimental studies. Factors that lead to the ultimate departure of a Chondrichthyan from a nursery ground (if the species has a nursery ground to begin

with) are also unclear. However, it can be assumed that nurseries (both inshore/offshore) also double as juvenile foraging grounds, and that these areas are distant from adult foraging grounds to avoid possible cannibalism (Dingle 1996).

Habitat descriptions for the nurseries of the five species highlighted in this thesis have not been described, and research into benthic imagery with a special look into these locations is suggested, to see if a habitat pattern can be established. Studies that manipulate these possible nursery selection variables may allow for better understanding of why some habitats are suitable as nurseries while others are not, and can possibly help restore degraded nursery locations. However, although the lack of nurseries found in the five chimaera species could be due to fisheries missing these areas (i.e. surveys are not done there), they could also not have been found because they simply do not exist for deeper chimaeras. These species all lay eggs, and could possibly not have a specific area to lay these eggs as the habitat gets less varied the deeper you go. The eggs also lack tendrils, something other sharks use to help anchor the egg to a specific structure, which suggests that these animals may wedge their eggs between two surfaces (e.g. two rocks) or bury their eggs to “anchor” them.

### **3.2. ADULT HABITATS**

Trawl surveys showed that the geographic range of *Hydrolagus novaezealandiae* overlaps with that of *Hydrolagus bemisi*, exhibiting differences in depth of occurrence. *Hydrolagus bemisi* was more prominent throughout the Campbell Plateau, near the Antipodes/Bounty Islands and on the western side of the South Island, while *Hydrolagus novaezealandiae* has patchier populations (i.e. *H. novaezealandiae* tows on average were less dense than *H. bemisi* tows). This habitat overlap may be due to both species being predominantly benthic feeders (Dunn et al. 2010b).

*Callorhynchus milii* had a compact range, staying within the shallow waters of New Zealand, and never being caught on the Chatham Rise, Campbell Plateau or Challenger Plateau. Why the areas around Christchurch (Pegasus Bay and Banks Peninsula), near the Karamea Bight and the Te Waewae Bay have continuous high density catch rates are unknown, as in-depth bathymetry of those locations has not yet been done. I believe salinity the relatively warm surface currents may be factors that have yet to be considered, as these areas are near rivers that meet the Southwest Pacific Basin and Tasman Sea.

Depth distribution within a species (e.g. Wetherbee et al. 1996, Pikitch et al. 2005, McAuley et al. 2007, Andrews et al. 2009) can be from predator avoidance, although the predators of these chimaeras are poorly known (Guallart et al. 2015) besides ling (Dunn et al. 2010; Stevens et al. 2011).

## **Mating Ground**

With no definition found in the literature, we proposed that mating grounds be defined as a spatially and temporally persistent location (unlike a mating aggregation, which can move); meeting for copulation in a different place every year isn't logical when optimizing this a good idea. Of the five species analyzed, all but one (RCH) showed tows meeting mating ground area composition criteria. Upon further inspection, most of these tows were single-digit numbers of different sex individuals. These could be chance encounters with the opposite sex, and could suggest that chimaeras not have a specific mating grounds due to sperm storage. While ubiquitous, these areas should be the focus of future reproductive studies to see if mature females/males caught in these locations are sexually active.

## **Mating Ground: Aggregation**

This habitat was not able to be distinguished from the trawl database without detailed stomach content and reproductive data, which were not available. *Callorhynchus milii* is known to migrate to shallow inshore waters in spring and aggregate for mating (Francis 1997); occurrence in Te Waewae Bay and near Invercargill could possibly denote this inshore migration, however this is just speculation.

## **Mating Ground: Lek**

We have defined a lek as a location that is a spatially and temporally persistent, like that of a mating ground. However, a lek has a higher proportion and density of males than females. Höglund and Alatalo (1995) provided a review of lekking, describing 21 fish species who practice lek-like mating. With so many fish species participating, logic points to leks possibly being associated with extreme sexual dimorphism. Chondrichthyans do not express sexual dimorphism (save for the external claspers of males), but chimaeras might qualify for lek-like mating due to theirs (males with frontal tenaculum and pelvic claspers).

We did not find any leks in four of the five species, but found 45 tows that met the lek criteria in *Hydrolagus novaezealandiae* (GSH). Of these 45 tows, only one (kah1207\_13) was of particular interest with 41 large males, 13 large females, 26 small males and 4 small females. These tows seem most likely to be chance due to otherwise low numbers and no records elsewhere in other species. With a regular occurrence of males and females, it does not seem like chimaeras would need leks to successfully reproduce. Not much is known about leks in regards to Chondrichthyans because lek-like mating systems have never been described for elasmobranchs. In fact, multiple paternity in Chondrichthyans exists (Gubili et al. 2012; Byrne and Avise, 2012) argues against lek-like mating.

It seems that a region termed the shared offshore foraging area (SOFA) is the only documented literature of a possible lek-like mating system in elasmobranchs (Jorgensen et al. 2012), but even that theory has informational gaps (Domeier and Nasby-Lucas, 2013).

It is challenging to ascribe any behavior as lek-like in the absence of visual observations. The seasonal constriction of SOFA and those locations found in our own data could be due to the pursuit of a seasonally available prey. An expedition to these regions during the constriction could identify the presence of prey aggregation, but again, the absence of behavioral observations deems it impractical to assign these areas as lek-like until such.

### **Food aggregation with possible mating**

There is not much literature on the potential relationship between mating grounds and food aggregations, but there is an ecological connection that could be there and that, as scientists, we are missing. This unseen relationship could be important; for example, mating grounds could be linked by food (prey) and our fisheries could unknowingly wipe prey. It is not unreasonable to think this an uncommon relationship, and probably seen in higher trophic level sharks, but it is very rarely measured, if ever.

With a higher trophic level shark, such as *Carcharodon carcharias*, the connection between prey abundance and predator occurrence is visually obvious (e.g. great white shark patrolling of seal islands),

but with a species whose life history and overall biology we know so little about (e.g. chimaeras), fisheries could be doing damage to reproductive dynamics of a species without knowing it.

Dedicated research that takes into account stomach samples, bycatch samples in association with Chondrichthyans and reproductive status are necessary to discern this stage from an exclusive foraging ground. A recent publication regarding whale sharks in St. Helena (Clingham et al. 2016) provides preliminary evidence (observations) that whale sharks use the habitats around St. Helena for feeding and mating.

### **3.3 WHERE ARE THE FEMALES?**

More tows were dominated by males for all five chimaera species. The difference between male and female dominant tows was roughly two times or more, with the most extreme being 321 male dominant tows to 820 female dominant tows in *Hydrolagus bemisi*. The relative absence of females might be because they are elsewhere or they are dead.

“Elsewhere” means outside of the time and space that the trawl surveys have occupied; i.e., it could occur within the surveyed area, but not at the time that the survey ship was present. The females could be avoiding areas with males to rest after giving birth, on other feeding grounds, or getting to a nursery/pupping ground quickly to give birth, and then returning slowly due to exhaustion.

Yet, if the above scenarios are true, we have not found evidence pointing to either. It could be that we are just not looking for these scenarios and therefore overlooking them. Perhaps there are regions, or depths, that provide a safe haven for mature females from aggressive males during mating season (Pratt and Carrier 2001; Sims et al. 2001). One way to test this is to subtract juvenile females from these dominant tow numbers and see how many mature females there are. The cause of male dominant tows seen in all species are unknown.

Another potential cause of sex ratio biases in catches is refuging behaviour. Thus far, refuging behaviour has been observed in only a few elasmobranchs (Sims 2005) and appears to be a behavior predominantly undertaken by females, aggregating in a habitat (e.g. deep holes, open caves, etc.; McLaughlin and O’Gower, 1971; Sims et al. 2001). Generally, individuals rest in the designated “refuge” during the day prior to nocturnal or crepuscular foraging excursions. The factors leading to

this behavior remain unknown, but often result in spatial sexual segregation (Sims 2005). Sexual segregation due to refuging behaviour could have implications for fisheries management, as it may skew species abundance, distribution and habitat use between the sexes, therefore altering sex ratios in specific regions. However, this dataset found that males had more dominant tows (6173 tows) than female dominant tows (2140 tows). Male chimaeras could possibly be exhibiting refuging behaviour, but no literature exists on male Chondrichthyans and refuging behaviour.

### 3.4 CONCLUSION

Over the last few decades, much effort has been devoted towards quantifying and reducing bycatch in marine fisheries, with an emphasis on commercial fisheries. There has been a particular focus on Chondrichthyans given that bycatch is a frequently listed threat for them on the International Union for the Conservation of Nature Red List. There are still many gaps in our basic understanding of the biology and ecology of deep-sea fishes. The shortage of ecological information on deep-sea fish assemblages makes it difficult to effectively manage these resources. Fisheries are more effective than ever at fishing at deeper depths (Morato et al. 2006; Villasante et al. 2012); with shallower resources declining, it is expected this will only continue (Morato et al. 2006; Villasante et al. 2012).

In the absence of quantitative estimates of fish population numbers and the effect of fishing, fishery managers have used risk assessment to determine which species should be the focus of concern. This was completed for New Zealand in 2015 (Ford et al., 2016). From highest to lowest risk, the five chimaeras in this study were ranked by Ford et al. 2016 as: *Callorhynchus milii* (ELE) and *Hydrolagus novaezealandiae* (GSH) share the same score, *Harriotta raleighana* (LCH), *Hydrolagus bemisi* (GSP), and *Rhinochimaera pacifica* (RCH). On the basis of my results, I would suggest raising GSP's relative risk, given the vulnerability of possible pupping grounds. There are also habitats that should be the focus of future research (pupping grounds in particular), to determine if these specific locations are indeed valuable and in need of protection from fishing and other human impacts.

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