An investigation of spatial-temporal diel changes in *Loligo reynaudii* catch rates in the commercial squid jig fishery of South Africa

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Summary

Loligo reynaudii (chokka) squid has been jigged commercially on the South African South-southeast coast since 1982. Starting in 2019, a chokka-directed hydroacoustic survey programme has formed part of scientific efforts to best inform the management of this fishery, mainly focussed on surveying at daytime during October-November, on the main fishing grounds between Plettenberg Bay and Port Alfred. However, it has so far remained unclear whether this programme may be improved in terms of spatial-temporal focus, to better survey acoustically detectable aggregations of adult squid throughout the year. Considering that commercial jig catches similarly depend on the prevalence, intensity and duration of aggregations; and assuming *standardised* Catch Per Unit Effort (CPUE) to be a representative measure of local abundance and proportional representation of regional population distribution: this study employed statistical modelling to specifically investigate whether, on the commercial squid jig fishing grounds of South Africa, there is: (1) an effect of diel period on chokka CPUE; (2) seasonal variation in any effects of diel period on CPUE; and (3) spatial variation in any effects of diel period on CPUE between seasons and years. The data used were DFFE (South African Department of Forestry, Fisheries and the Environment) commercial session-level squid jig catch logbook records.

A *tweedie* generalized additive model was applied following an iterative semi-inductive modelling approach, for an optimal account of data non-linearity and non-normality when estimating CPUE as a function of relevant space-time variables. The data were limited, *inter alia*, to 2006-2022 sessions conducted purely at day/night between 20-29°E. The final model explained 24.4 % deviance and all terms were statistically significant in their effect on the response ($p<0.05$).

There were three main findings when estimating relevant terms' marginal effects. Firstly, chokka concentrations are greater at day than night. Secondly, there is clear seasonality in the aggregated proportion with a single greater daytime and lesser nighttime peak in annual spawning concentrations, around October-December. Thirdly, CPUEs involved varying spatial-temporal complexity while being greater at day than night across most of the fishing grounds for most of the average year.

The main takeaway was a dismissal of any notions that acoustically surveyable, large aggregations of squid may likely be found consistently in areas and at times other than when-where acoustic efforts have typically been expended in late spring so far, on inshore spawning grounds targeted by the commercial jigging fleet.

Recommendations for future research include accounting for session-level variations in relevant oceanographic parameters when modelling session-level jig CPUE.

Keywords: commercial CPUE, *Loligo reynaudii*, spatial-temporal, diel, modelling

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List of Abbreviations

MARiS – Marine and Antarctic Research centre for Innovation and Sustainability

FSAM – Fishery Stock Assessment Model

DFFE – South African Department of Forestry, Fisheries and the Environment

DFFE:FB – Fisheries Management Branch of the South African Department of Forestry, Fisheries and the Environment

MARAM – The University of Cape Town's Marine Resource Assessment and Management Group

Squid SWG – Squid Scientific Working Group at the Fisheries Management Branch of the South African Department of Forestry, Fisheries and the Environment

ML – Mantle Length

NM – Nautical Mile

Chapter 1: Introduction

Studying marine biotic populations and their ecology is becoming increasingly vital for social-ecological sustainability. In ~1800, the British industrial revolution heralded an age of rapid globalisation, industrialisation and technological advancement, marking the start of exponential human-induced pressures on local-global ecosystems (McNeill 2000, Crutzen 2002, Folke et al. 2016). Since then, research and monitoring has been acknowledged as crucial in ascertaining and keeping up to date on the vulnerability and susceptibility of species and their populations and associated ecosystems to becoming ecologically impotent (Baker et al. 2019, Tollefson 2019, Hogue and Breon 2022). This is especially the case when addressing the exploitation of marine living resources in present contexts of growing human populations, uncertain future climates and an increasing focus on opportunities in the oceanic Blue Economy (Hoegh-Guldberg and Bruno 2010, Luypaert et al. 2020, Hidalgo et al. 2022).

Contemporary approaches in marine fisheries science and management include the assessment of stock populations according to themes of present and postulated future environmental variability (Moustahfid et al. 2021, Hidalgo et al. 2022). However, it can never be concluded that all is known about the species themselves (Hoegh-Guldberg and Bruno 2010, Pinsky et al. 2018). This makes it necessary for relevant scientific knowledge to be grounded in recent ecological findings for an ecosystem-based approach to fisheries to be optimally effective in the present-day (Boesch 1999, Jennings 2005, Hidalgo et al. 2022). As a consequence, fisheries research needs to involve the continual monitoring of species behaviour in relation to short and long-term change in these species' living environments (Hoegh-Guldberg and Bruno 2010, Moustahfid et al. 2021). This is especially true for species such as squid (Rodhouse et al. 2014, Luypaert et al. 2020), a colloquial grouping of approximately 290 species in the cephalopod Order Teuthoidea (Arkhipkin et al. 2015).

1.1 Coleoid cephalopods: An overview

Coleiod cephalopods (squid, cuttlefish, octopi) are ubiquitous in the global ocean, found from the tropics to the poles (Fries 2010, Rosa et al. 2019); and occur in benthic, benthopelagic and pelagic habitats, from 0 to >5000 m depths (Clarke 1996, Boyle and Rodhouse 2005, Guerra et al. 2014). And, compared to their longer living and slower growing teleost sympatrics, these

~800 living species have a relatively high degree of short-term plasticity relative to environmental variability (O'Dor and Webber 1986, Boyle and Boletzky 1996, Rodhouse et al. 2014, Arkhipkin et al. 2015).

1.1.1 Biology: Traits and Strategies

Coleoids have evolved a strategy of living fast and dying young by growing as fast as possible, to reproduce as soon as environmentally feasible within their evolutionary biological constraints (O'Dor and Webber 1986, Anderson et al. 2002, Rodhouse et al. 2014). This involves efficient food to body mass conversions and fast growth rates (Wells and Clarke 1996, Vidal et al. 2014), but relatively short life spans (Rodhouse 1998, Wood and O'Dor 2000) with a build up to and exhibition of monocyclic spawning (Rocha et al. 2001), ending in senescence and death (Robin et al. 2014). However, there is also relative divergence in biological traits between and within taxa. Oegopsid, neritic-oceanic squids such as *Illex illecebrosus* exhibit a near-absence of courtship rituals when mating and can spawn in midwater as eggs are deposited in neutrally buoyant, free floating masses (O'Dor and Balch 1985, O’Dor and Dawe 2013). On the other hand, benthic spawners such as the mostly neritic myopsid squid *Doryteuthis* (*Loligo*) *pealeii* deposit and attach their egg capsules individually to submarine substrates following multi-faceted, pre- and post-copulative maternal selection of paternities during spawning events (Shashar and Hanlon 2013). With all coleoid taxa, the size and number of eggs deposited partly signify phylogenetic strategies to maximise progeny survivability at the cost of parent fecundity or vice versa (Ibáñez et al. 2021).

Divergent coleoid life histories involve differing typologies of hatchling dispersal, competition, and predation risk. Holopelagic and merobenthic species deposit relatively smaller eggs in larger numbers with embryos eclosing (i.e., ‘hatching’ or emerging) as paralarvae hatchlings, meroplanktonic organisms with limited active motility. This gives hatchlings relatively greater dispersion potential at the cost of increased vulnerability to abiotic risks and pressures (e.g., adverse conditions) compared to juvenile hatchlings (Young and Harman 1988, Villanueva et al. 2016, Vidal and Shea 2023). Holobenthic and meropelagic species, on the other hand, deposit relatively larger eggs in smaller numbers with embryos emerging as juvenile hatchlings, miniature and weaker versions of the species’ adult forms. As they ‘hatch’ at a relatively larger size in presumably suitable habitats, such individuals arguably have greater survival fitness and potential than paralarvae hatchlings. However, this also puts them in direct competition with any larger, stronger conspecific sympatrics as they naturally have relatively limited ranging capabilities during early development stages (Villanueva et al. 2016, Ibáñez et al. 2021, Vidal and Shea 2023).

Whether any cohort successfully survives, grows and effectively reproduces, however, depends on the environments individuals are subjected to during each phase of their lives (Robin et al. 2014, Rodhouse et al. 2014).

1.1.2 Environmental influences

Oceanographic variability affects cephalopod populations' present and future structure, distribution and abundance (Semmens et al. 2007, Rodhouse et al. 2014). Species have evolved in their life history concomitant to the environment and environmental variability of their ontogenetic niches (Werner and Gilliam 1984, Rodhouse et al. 2014, Fokkema et al. 2020). This has led to extants being adapted to survive and perform optimally within a specific range of environmental conditions, including pH, salinity and (especially) temperature[1] (Rodhouse et al. 2014, Vidal et al. 2014, Borges et al. 2023). Biogeographically, these ambient conditions form part of meso-synoptic oceanographic processes to which cephalopods adapt accordingly and, in some cases, even employ to better succeed as species (Semmens et al. 2007, Rodhouse et al. 2014).

Interplays between life history, ontogeny and environmental variability lead to spatial-temporal changes in the local-regional abundances of cephalopod species (Robin et al. 2014, Rodhouse et al. 2014, Vidal and Shea 2023), with examples including *Doryteuthis* (*Loligo*) *gahi* in Falkland Island waters (southwest Atlantic) (Arkhipkin et al. 2004a) and *Loligo forbesii* and *Loligo vulgaris* in western European waters (northeast Atlantic) (Laptikhovsky et al. 2022). These and many other loliginid populations tend to largely be locally retained in their lifetime distributions, completing ontogenetic migrations hundreds of kilometres long, between

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[1] Cephalopods are ectothermic poikilotherms and thus strongly influenced by temperature in their 'pace of life' (Hoving et al. 2014, Rodhouse et al. 2014, Vidal et al. 2014). With a mean body temperature towards the upper limit of the species-specific optimal thermal range, individuals tend to have faster growth rates (Moltschaniwskyj 2004, Leporati et al. 2007), higher metabolic rates, higher oxygen-energy demands (Melzner et al. 2006, Melzner et al. 2007) and shorter life spans (Forsythe and Hanlon 1988, Wood and O'Dor 2000, Takahara et al. 2017).

inshore nursery/spawning and offshore feeding grounds (O'Dor 1998, Boyle and Rodhouse 2005).

Maturing Falklands *D. gahi* vary in how far and deep and for how long individuals remain offshore as maturing periods depend, in part, on the extent, bathymetry and seasonal isolation of near-bottom feeding grounds in preferred warm water layers of the Transient Zone. This leads to the Falklands *D. gahi* population being dynamically in tune with seasonal fluxes in the thermal homogeneity of inshore to offshore and bottom to surface water layers (Arkhipkin et al. 2004a, Arkhipkin et al. 2004b). In western Europe, temperature seems to have a similar influence on *Loligo* populations as Laptikhovsky et al. (2022) showed corresponding between-season shifts in the location of optimal bottom temperatures and *L. forbesii* – *L. vulgaris* spawning and nursery grounds between November and July. This allows for retention and development of early life stages in coastal habitats with, *inter alia*, thermal resources conducive to embryonic development and exponential growth, and sufficient sheltering from predation/fouling and, or shear stress (Arkhipkin et al. 2000, Boyle and Rodhouse 2005, Laptikhovsky et al. 2022).

These examples partly allude to coleoid cephalopod populations naturally having a ‘boom or bust’ quality. Each generation is ecologically geared towards optimising on favourable environmental conditions. However, this also means cohorts are inherently vulnerable to collapse when unfavourable conditions are prevalent. And such vulnerability is exacerbated especially for exploited coleoids, species characterised by a limited number of intergenerational cohorts within individuals’ lifetime (consequent to their typical natural lifespan of ~1-2 years) (Rodhouse et al. 2014, Arkhipkin et al. 2015, Sauer et al. 2021). That is why it is crucial to *inter alia* also consider coleoid cephalopods in the context of their supportive role in contemporary societies (Clarke 1996), especially species which are both intrinsic to a changing ocean and of local-global economic importance (Hunsicker et al. 2010, Ospina-Alvarez et al. 2022).

1.1.3 Fisheries

Cephalopods have been valued in cultural and culinary terms as early as 4000 years ago. Depictions are found in the artwork of early civilisations and ancient literary works pertain, *inter alia*, to cephalopod biology and harvesting (Schmitt 1965, Mouritsen and Styrbæk 2018, Nakajima et al. 2018). These cultural stores of non-verbal, intergenerational knowledge contributed to cephalopods being regarded as fascinating creatures and utilised for human sustenance starting within regions such as East Asia, southeast Asia and southern Europe, progressively up to the global scale of today[2] (Pierce and Portela 2014, Mouritsen and Styrbæk 2018, Nakajima et al. 2018, Ospina-Alvarez et al. 2022).

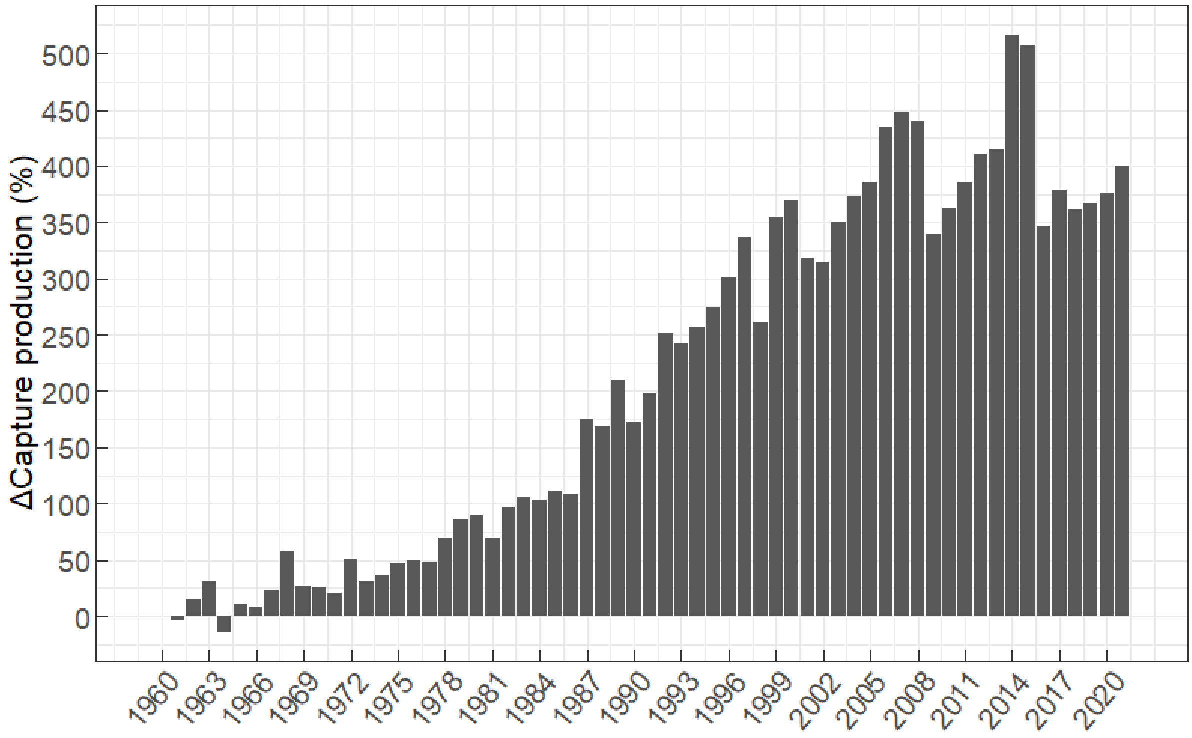

Figure 1: Percentage difference in annual estimates of global cephalopod capture production relative to reported landings in 1960 (FAO 2023).

Pre-2022 global cephalopod capture production has grown annually by an average of around 51,500 tonnes (~3.48 %) since 1960, reaching the contemporary peak of ~4,850 000 tonnes total landed in 2014 (FAO 2023). Relative to the combined cephalopod landings in 1960 (~787,000 tonnes), this ~516 % stagger-paced increase from 1960 to 2014 (See Figure 1; FAO 2023) seems to have been partly concomitant and consequent to global trends of 'fishing

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[2] "Although squids are not a popular food, except among the Japanese and some other enlightened peoples, these organisms are among the most numerous and underexploited of the edible animals in the sea…" (Tont and Delistraty 1977, p. 251).

down' marine food webs (Pauly and Palomares 2001); fishery disciplines' notice of largely global cephalopod abundance and biomass increases, and declines to slow recovery rates of longer-lived fishing stocks (e.g., groundfish) (Caddy and Rodhouse 1998, Doubleday et al. 2016); greater prevalence of fishers' use of motorized vessels (Rousseau et al. 2019); development of locally to regionally more optimal harvesting technologies (e.g., Nguyen and Nguyen 2022); successive shifts in international harvesting with the stagger and collapse or recovery of regionally prominent, cross-boundary cephalopod stocks (Arkhipkin et al. 2015); and growth in domestic to global commercial markets (Pierce and Portela 2014, Ospina-Alvarez et al. 2022). Since the 2014 peak, however, annual capture production seems to have dropped and mostly stabilised again at levels similar to landings made during the late 1990's-early 2000's (See Figure 1, Figure 2; FAO 2023).

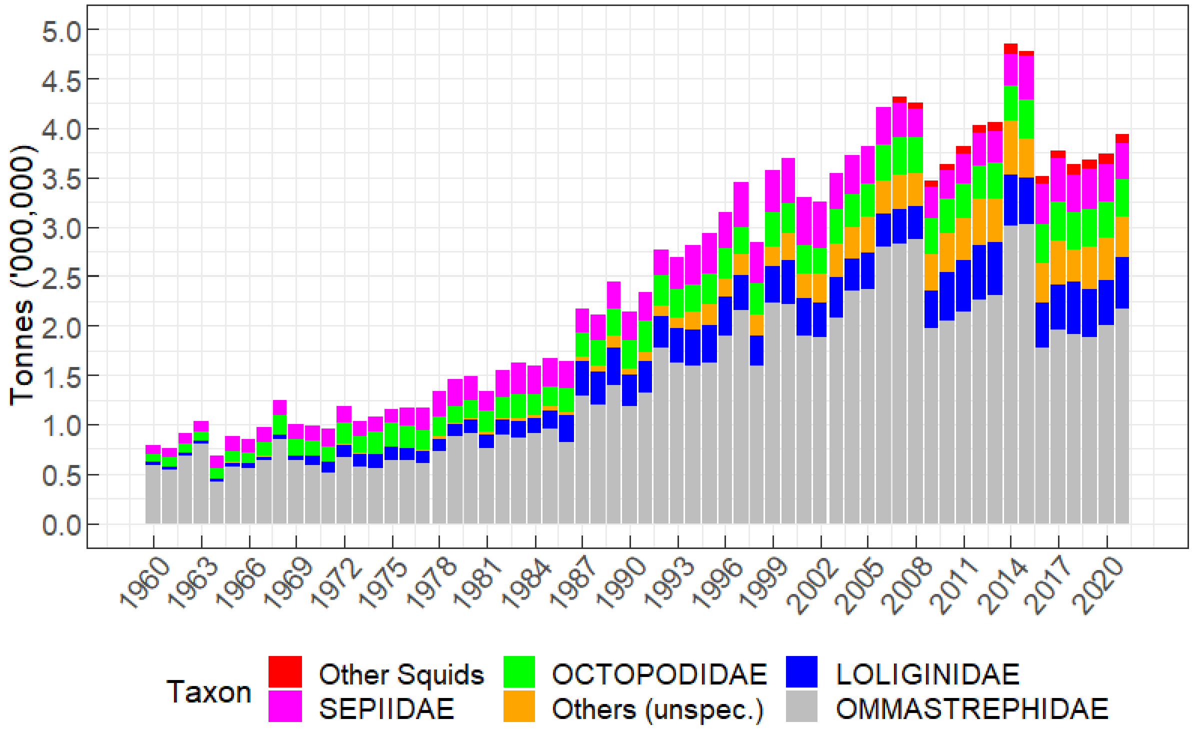

Figure 2: Annual estimates of major cephalopod taxa's global capture production from 1960 to 2021 (FAO 2023).

In 2021, total recorded cephalopod landings (~3,930 000 t) constituted between 4 and 5 percent of global marine fisheries capture production. Landings were mostly made by China (~29 %), Peru (~13 %), Vietnam (~9 %) and Indonesia (~6 %) (FAO 2023). China also dominated as a relative producer of cuttlefish (Sepiidae: ~34 %; ~126,205 t), oceanic squid

(Ommastrephidae: ~41.6 %; ~900,792 t) and incirrate octopus (Octopodidae: ~28.2 %; ~106,297 t). Most neritic squid (Loliginidae) was landed by Indonesia (~39.6 %; 204,156 t), Other squid by Russia (~99.8 %; ~76,444 t) and Other (unspecified taxa) by Vietnam (~84.9 %; 359,500 t). For taxon families overall, global 2021 landings mostly consisted of ommastrephids (~55 %; ~2,167 844 t) and then loliginids (13 %; ~515,296 t) and Others (unspecified taxa) (10 %; ~423,596 t) (See Figure 2; FAO 2023). In part, these estimates allude to contemporary prevalence of Chinese distant-water fleet operations in major cephalopod fishing industries (Arkhipkin et al. 2023, Seto et al. 2023); the marked contribution of unspecified taxa reported by Vietnam (FAO 2023); and continual prominence of the ommastrephid and loliginid squid families as global cephalopod fishing stocks (Rodhouse and Nigmatullin 1996, Jereb et al. 2005, Arkhipkin et al. 2015).

It remains true that certain species and species groups are a main focus of exploitation (FAO 2022, FAO 2023), notwithstanding any uncertainties around the actual complete magnitude and variety of marine taxa that are harvested globally (Pauly and Zeller 2016). Compared to the long-finned (Loliginidae) squids, short-finned (Ommastrephidae) squids have a lower market value in Europe (Jereb et al. 2010), a major global cephalopod trader (Ospina-Alvarez et al. 2022), but may be caught in amounts several magnitudes higher with typically larger 'booms' in fishery recruitment after periods of favourable regional climates (Rodhouse et al. 2014, Arkhipkin et al. 2015). Notable ommastrephid and loliginid fisheries include landings of the short-finned *Dosidicus gigas*, *Illex argentinus*, *Nototodarus sloanii*, *I. illecebrosus* and *Todarodes pacificus*; and long-finned *L. forbesii*, *D. gahi*, *Loligo bleekeri* and *D. pealeii* (Arkhipkin et al. 2015). These and other squid species may be taken as bycatch with operations by non-squid fisheries or targeted directly (Rathjen 1991, Arkhipkin et al. 2015).

Targeted squid fishing methods include handline jigging, machine jigging, purse seining, midwater trawling and bottom trawling during night and, or daytime. Method advantages-disadvantages include the potential bulk of catches made per haul using trawls. Jigging catches, on the other hand, typically result in a better-quality product (less fishing-gear damage to soft tissue) and therefore tend to involve a higher ex-vessel price per unit sold, apart from jigging operations involving relatively low to a near-absence of bycatch and damage to benthic environments (Rathjen 1991, Jereb et al. 2005, Arkhipkin et al. 2015). And nighttime operations typically employ artificial lighting when carried out in upper water layers (e.g., jigging and purse seining), taking advantage of relevant squid taxa being attracted to light when feeding relatively near the surface after dusk (Rathjen 1991, Rodhouse et al. 2014, Arkhipkin et al. 2015). However, whether harvesting is done during night and, or day seems to partly depend on fishing decision-makers' (e.g., skippers') experience and knowledge on the realities of target squid stocks' diurnal-nocturnal prevalence and associated catch rates at the time and in the area of operation (Rathjen 1991).

1.1.4 Management relevance of the study

Squid ecology requires relevant fisheries managers to ideally be informed day-to-day and adaptive management to be implemented month-to-month. As exploited squids are typically short-lived, fast growing and 'semelparous' (Boyle and Boletzky 1996, Rocha et al. 2001, Arkhipkin et al. 2015), short-term changes could potentially have relatively long-term implications for the optimal, sustainable utilisation of these fishing stocks (Hoegh-Guldberg and Bruno 2010, Rodhouse et al. 2014). This warrants an understanding of short-term change in squid behaviour-environment relationships to optimise relevant fisheries management practice. And relatively basic measures include variations within and between diel time periods (Rodhouse et al. 2014, Arkhipkin et al. 2015).

1.2 Diel of a squid

Diel can be defined as "involving a 24-hour period that usually includes a day and the adjoining night…" (Merriam-Webster 2023).

Individual fauna are mediated in the proportionate expenditure of their circadian, activity-rest budgets by the state of ambient conditions (Mather and O'Dor 1991, Folk et al. 2006, Tessmar-Raible et al. 2011). Any changes in ambient state (e.g., temperature, salinity, light) may serve as a cue for potentially immediate or imminent *risk* (e.g., predator presence, abiotic stress) and, or *benefit* (e.g., food availability, reproductive opportunity), depending on the sensory acuity with which an organism perceives its environment. Such ambient-type change naturally entails an entrained biological response or responses (e.g., rest, feeding, fleeing and, or migration) by the perceiving party (Tessmar-Raible et al. 2011, Meisel et al. 2013, Cohen et al. 2021).

In squid, oceanic and neritic species are known to carry out diel migrations as individuals optimise their temporal success in horizontal and, or vertical space (Rodhouse et al. 2014, Arkhipkin et al. 2015, Hanlon and Messenger 2018). Sub/adult *D. gigas* (Ommastrephidae) optimise feeding success, predator avoidance and energy expenditure through diel associations with mid-water, oxygen-limited zones during ontogenetic horizontal migrations in the Gulf of California and California Current Systems (Gilly et al. 2006, Rosa and Seibel 2010, Stewart et al. 2013). These squids employ metabolic suppression to frequent such hypoxic environments predominantly during diurnal time periods (Gilly et al. 2006, Rosa and Seibel 2010, Stewart et al. 2013), when their main mesopelagic prey mostly occupy similar depths (Robison 1972, Markaida and Sosa-Nishizaki 2003, Gilly et al. 2006). These environments also allow for prey capture with minimal energy expenditure relative to metabolic gain (Rosa and Seibel 2010), and respective avoidance of and escape from pelagic competitors and predators with limited tolerance for oxygen-deficient conditions (Gilly et al. 2006, Stewart et al. 2013). In the family Loliginidae, mature *L. vulgaris* range widely when feeding at night on their inshore spawning grounds in southern Mallorca, northwest Mediterranean. However, squid become constrained in their spatial movement range when aggregating to spawn at a potentially different site each day (Cabanellas-Reboredo et al. 2012a).

These above patterns and behaviours exemplify the mechanistic mediation of within-species and between-species spatial movements. Day-to-day and season-to-season, such mediation optimises relevant ontogenetic distributions and abundances towards ultimate and effective reproductive success (Tessmar-Raible et al. 2011, Rodhouse et al. 2014). In addition, this influences the spatial-temporal accessibility and susceptibility of populations to research sampling and, or fisheries harvest (Rathjen 1991, Boyle and Rodhouse 2005). In the northwestern Atlantic United States mid-water *I. illecebrosus* squid otter-trawl fishery, *I. illecebrosus* squid catches comprise, on average, of consecutively heavier individuals in the afternoon, morning and evening (Bochenek and Powell 2021). Bochenek and Powell (2021) presumed these variations in catch to be the result of size-related spatial segregations in diurnal hunting strategies. Larger *I. Illecebrosus* would migrate downwards around dawn to stay at greater depths for larger parts of the day, where they are able to hunt correspondingly bigger prey if available, before migrating towards the surface around dusk (Ivanovic and Brunetti 1994, Bochenek and Powell 2021). Similar to *L. vulgaris* in southern Mallarco, *L. reynaudii* follow a predominant pattern of dispersing shortly after sunset to feed and, or rest at night before returning to exhibit aggregate behaviour when spawning mostly during the day on the southeast coast of the South African inshore (Sauer and Lipiński 1991, Sauer et al. 1992, Sauer et al. 1997). However, it has so far not been established whether *L. reynaudii* catches reflect this diel pattern in any way despite this species being, *inter alia*, of notable local commercial fisheries concern (Githaiga-Mwicigi 2023).

1.3 *Loligo reynaudii* Orbigny, 1839–1841 in South African waters

One of the 47 known species in the Loliginidae family (Hoving et al. 2014), *L. reynaudii* occurs along the southern African continental shelf: from southern Angola, ~500 km North of the Cunene River to the Great Fish River in Eastern Cape, South Africa. This distributive range constitutes a metapopulation characterised by limited genetic variability, with sufficient dispersive and, or migratory gene flow between the Angola-Benguela-Agulhas Bank regions[3] (Roberts 2005, Lipiński et al. 2016, Van Der Vyver et al. 2016). However, interplays between environmental variability and short-term cephalopod plasticity lead to subpopulation-level phenotypic divergence between these regions. In South African waters, for example, squid biology is largely governed by prevailing oceanography of the Western Agulhas Bank – West Coast and Eastern to Central Agulhas Bank (Kirkman et al. 2016, Lipiński et al. 2016, Van Der Vyver et al. 2016).

1.3.1 Biology and the environment

Individual life histories and population dynamics vary between the West to southwest (Port Nolloth-Cape Agulhas) and South to southeast (Cape Agulhas-Port Alfred) coast. While juveniles can be up to 240 mm in Mantle Length (ML) (See Figure 2(a) in Olyott et al. 2007), mature females are typically 100-180 mm ML and mature males can be 'small', 90 mm ML or reach a relatively large size of 250 mm ML while still immature (Augustyn 1989, Augustyn et al. 1994). Despite this marked variability in the size-at-maturity, specimens tend to exhibit slower growth rates and mature at larger sizes on the western compared to eastern Agulhas

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[3] The Agulhas Bank may be defined to sectionally comprise of the Western Agulhas Bank (Cape Town-Cape Agulhas, ~18-20°E), Central Agulhas Bank (Cape Agulhas-Knysna, 20-23°E) and Eastern Agulhas Bank (Knysna-Port Alfred, 23-27°E) regions. These regions collectively constitute >29,000 NM^2, a near-triangular shaped section of the African continental shelf extending South, offshore until the 1000 m isobath between Cape Town and Port Alfred (Japp et al. 1994, Olyott et al. 2006).

Bank. Also, bathymetrically, biomass is mostly limited to the ≤200 m isobaths in the East while squid can be found up to ~350 m deep on the West coast (Augustyn 1991, Augustyn et al. 1994, Roberts and Sauer 1994). And abundance seems to be limited by ≤8°C bottom temperatures and ≤3.5ml 1^{-1} bottom oxygen levels, conditions mostly prevalent to the West and sparse to the East of Cape Agulhas (Augustyn 1991, Roberts 2005).

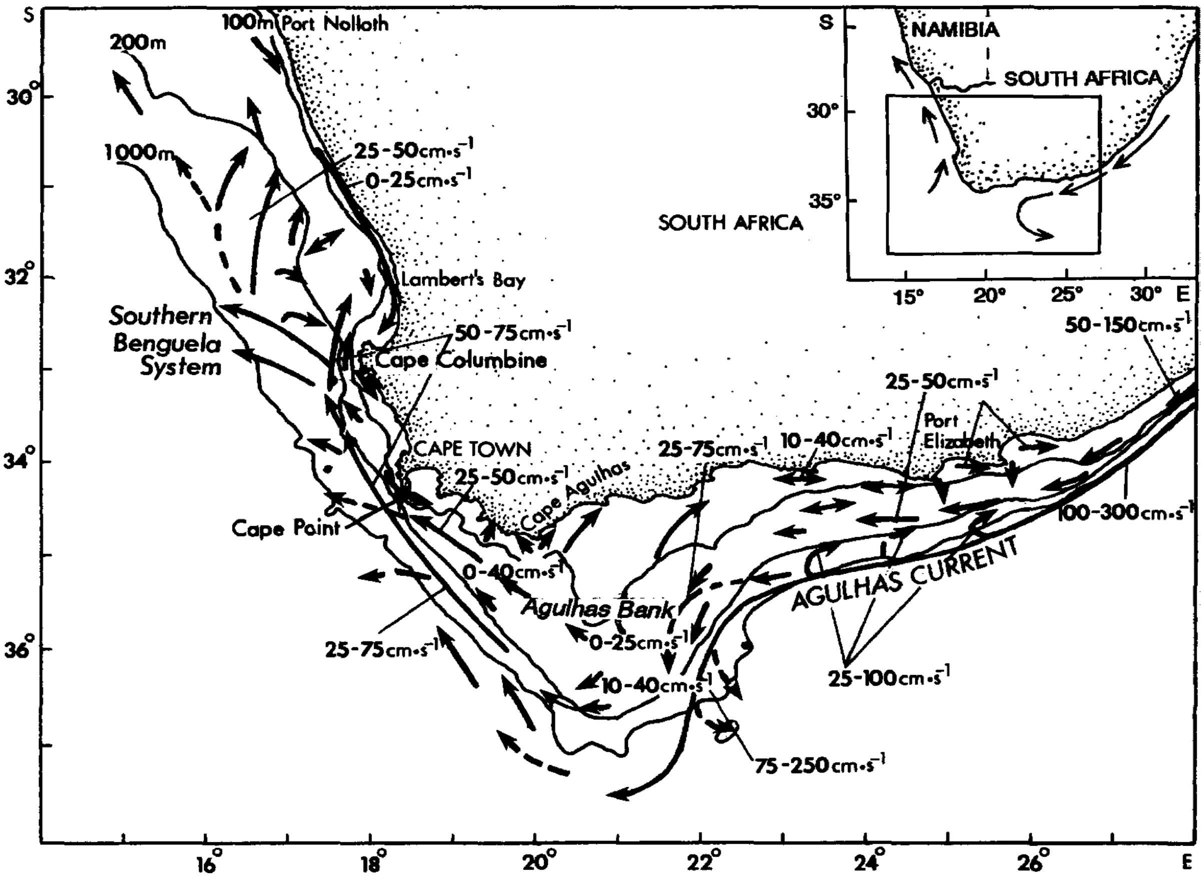

Figure 3: Map showing oceanographic features of note on the West to South-southeast coast of South Africa, including near-surface currents based on Acoustic Doppler Current Profiler data collected between November 1989 and January 1992. Adapted by Hutchings et al. (1995) from Boyd et al. (1992).

Interlinkages between *L. reynaudii* biology and regional oceanography are arguably due to prominent influence of dynamics in prominent boundary currents on the East to West coasts. With Figure 3 as an illustrative example (Boyd et al. 1992, Hutchings et al. 1995), the relatively cold (5-11°C) – slow (~0.2 m s^{-1}) equatorward-flowing Benguela Current is in the West (Augustyn 1991, Roberts 2005, Shillington et al. 2006, Van Der Vyver et al. 2016) and warmtemperate (9-24°C) – fast (∼2 m s^{-1}) southbound Agulhas Current in the East (Augustyn et al. 1994, Roberts 2005). Also, these current systems' interactions with the continental shelf break, predominantly shallower on the Agulhas Bank (~200 m) and deeper on the West Coast (~400 m), lead to relatively more frequent and larger-scaled coastal upwelling on the West Coast (Lutjeharms et al. 1989, Roberts 2005). These characterising oceanographic factors and their dynamics result in conditions which are, on average, more conducive to overall *L. reynaudii* success towards the East of its South African distributive range. And this leads to South African *L. reynaudii* life cycles notably depending on the Agulhas Bank regions, with a large to major proportion of the adult biomass found between 20°E and 27°E (Roberts and Sauer 1994, Roberts 2005).

L. reynaudii follows a merobenthic lifecycle pattern presumably over a ~13-month lifespan, reaching sexual maturity at <12 months (Lipiński et al. 2016, Lipiński et al. 2020, Durholtz and Glazer 2022, Vidal and Shea 2023). Early research seemingly indicates a seasonal pattern of annual but interannually variable 'squid runs' (Augustyn 1989, Augustyn et al. 1994, Lipiński 1998). In other words, there appeared to occur a predominantly West to East surge in areal inshore spawning from Plettenberg Bay (~23.3°E) to Port Alfred (~26.9°E), at least during austral spring/summer. Such a wave-like surge seemed to arise from pre-spawn squids migrating in bulk from feeding grounds mostly on the Central Agulhas Bank, Western Agulhas Bank and, or West Coast (Augustyn 1989, Augustyn et al. 1994, Lipiński 1998). Hence, this seemingly signified annual to multi-seasonal occurrence of a coordinated, large-scale West to East adult chokka migration (i.e., a largely synchronous spawning cycle at population-level) (Augustyn 1989, Augustyn et al. 1994, Lipiński 1998). However, more recent syntheses seemed to allude that adult migration and aggregation patterns are notably less straightforward and predictable (e.g., Lipiński et al. 2016).

The currently accepted scientific narrative seems to be that South African chokka subpopulations' adult life history stages are characterised by spatial-temporal regimes involving considerable complex stochasticity (Lipiński et al. 2016). Compared to the Central and Western Agulhas Bank, the Eastern Agulhas Bank seems to be characterised by greater proportional incidence of adults, at least during spring and autumn (Olyott et al. 2007). Arguably, this lends partial support to earlier 'squid run' notions and alludes to typical spawner preference for the Plettenberg Bay-Port Alfred inshore (Roberts et al. 2012, Lipiński et al. 2016). However, there appears to be no consistent trend of adult squids increasing in their degree of sexual maturity (i.e., >Gonadosomatic indices – GSI) moving from West to East. Rather, findings appear to have shown statistically notable indications of lesser or greater GSI in some 1° longitudinal areas $[\sim 20°E;\ \sim 27°E]$ during spring and, or autumn in some years (Olyott et al. 2006). In addition, eggs have been found from False Bay to Port Alfred-East London, up to mid-shelf (71-130 m) and even ~270 m depths (Roberts et al. 2012)[4]. Hence, current thought seems to be: reproduction occurs in a series of spatially and, or temporally separate spawning-hatching 'events' as adult squids are present and potentially spawn throughout the year across the Agulhas Bank (Olyott et al. 2006, Olyott et al. 2007, Lipiński et al. 2016); and, notwithstanding the incidence of extensive and, or deepwater spawning, aggregations are typically found in areas of the Plettenberg Bay-Port Alfred inshore, 22°45' to ~27°E (Roberts and Sauer 1994, Roberts et al. 2012).

Relevant embryogenesis constitutes a start to the *L. reynaudii* life cycle on the Plettenberg Bay-Port Alfred inshore area, as ~82 % of eggs are found at ≤70 m depth, with a peak in the biomass at 21-50 m within this region (Roberts et al. 2012, Robin et al. 2014, Vidal and Shea 2023). Following Augustyn et al. (1992) and Oosthuizen et al. (2002), development is optimal at 12-17°C as it results in minimal abnormalities; time-to-hatching is inverse to ambient temperature, ~50.1 days at 12°C and ~26.6 days at ~17°C; and egg mortality prevails at <10°C and >24°C. Work by Augustyn (1989) (cited in Augustyn et al. 1994, p. 145), Vidal et al. (2005) and Martins et al. (2010) indicated hatchlings emerge as paralarvae sized 2.30-2.43 ± 0.08-0.18 mm ML, with 3 to 4 days' worth of yolk reserves allowing for mortality only 6-8 days post-hatch, when incubated – reared at optimal temperatures (e.g., 16 ± 1°C – 16 ± 1°C or 15.60 ± 1.30°C – 16.59 ± 0.49°C). Such variable early-stage ontogeny makes apparent the dependence on temperature in the rate of embryonic development, hatchling yolk utilisation and potential hatchling survival time until first exogenous feeding. This alludes, *inter alia*, to

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[4] Such extensive and, or deepwater spawning is arguably consequent to prevalence of sub-optimal conditions (e.g., high bottom turbidity) in preferred spawning areas in conjunction with alongshore advection and, or nearshore to mid-shelf intrusion, through downwelling, of thermal resources conducive to spawning, egg deposition and, or optimal embryonic development (Roberts and Sauer 1994, Roberts et al. 2012).

endogenous hatchling state notably depending on ambient abiotic (e.g. temperature) to biotic (e.g., prey) dynamics throughout the paralarva phase.

The planktonic paralarva phase has been estimated to last around 2-3 months (Bruggeman et al. 2022). With no local ontogenetic retention or advective offshore loss due to absence of alongshore counter currents or current reversals, Plettenberg Bay-Port Alfred inshore hatchlings are subject to the predominantly west to southwest-flowing Agulhas Current (Roberts 2005, Martins et al. 2014, Jacobs et al. 2022a). Serendipitously, this leads to passive drift from major spawning/hatching grounds on the Eastern Agulhas Bank (EAB) to nursery/feeding grounds on the Central Agulhas Bank (CAB) (Roberts 2005, Martins et al. 2014, Jacobs et al. 2022a), proximate to a copepod (e.g., *Calanus agulhensis*) maximum at the "Cold Ridge"[5] (Huggett and Richardson 2000, Roberts 2005, Huggett et al. 2023). Although preferred paralarvae diets are thought to largely consist of *C. agulhensis* (Venter et al. 1999, Roberts 2005, Arkhipkin et al. 2015), cohorts arguably only cross an ecologically pertinent no-return threshold between sustenance and starvation under exceptional circumstances (Vidal et al. 2006, Martins et al. 2010, Martins et al. 2014). This is due to viable prey such as polychaetes, copepods and euphausiids (Venter et al. 1999) being typically found in sufficient quantities at appropriate times on the Agulhas Bank (Roberts 2005, Martins et al. 2010, Martins et al. 2014). In broader terms, these dynamics highlight the importance of the Agulhas Current's spatio-temporal East-West stochasticity in whether relevant *L. reynaudii* reach their nursery/feeding grounds successfully and in a competitively fit condition.

Early life-cycle success allows *L. reynaudii* to transition from paralarvae, on average, ~9 months prior to spawning, to ultimately progress into sexually mature and spawning adults barring non-senescent death (Sauer et al. 2013, Bruggeman et al. 2022). Following Young and Harman (1988), Robin et al. (2014), Bruggeman et al. (2022) and Vidal and Shea (2023), hatchlings 'graduate' to juvenile phase through morphometric development for and

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[5] The "Cold Ridge" may be defined as a quasi-permanent feature of upward doming in the thermocline, consequent to upwelled water being advected southwest, following the 100 m isobath, from the vicinities of Tsitsikamma, to Mossel Bay (Swart and Largier 1987, Boyd and Shillington 1994, Roberts 2005, Hancke et al. 2023).

ethological realisation of dexterous diel vertical migration between a lifestyle of "…demersal-by-day, pelagic-by-night…" (Bruggeman et al. 2022, p. 2). This allows, *inter alia*, for utilisation of a more diverse range of prey to optimally maximise meeting greater energy demands (Nixon 1985, Rodhouse and Nigmatullin 1996, Smith 2003, Markaida et al. 2008, Camarillo-Coop et al. 2013, Roura et al. 2023).

L. reynaudii may presumably hunt prey sized up to more than half their mantle length (Lipiński 1987). Lipiński (1987) found juvenile to subadult-sized squid (69-125 mm ML) to mostly prey on euphausiids in St Francis Bay, Eastern Cape. This differs from findings by Augustyn (1991), of a subadult (136-209 mm ML) preference for fish when maturing on the West Coast. Lipiński (1987) also found subadults to adults (126-240 mm ML) prefer fish and decapod crustacea (incl. euphausiids) in the St Francis Bay area. However, whether juvenile squid feed as they are able to on what is available while remaining to grow and mature on the CAB, or migrate to mature off the West Coast, or potentially return early to sexually mature on the EAB (Augustyn 1991, Roberts 2005, Lipiński et al. 2016), pre-senescent squid still predominantly migrate from West to East to spawn off the coast between Plettenberg Bay and Port Alfred (Olyott et al. 2006, Roberts et al. 2012, Lipiński et al. 2016).

1.3.2 Inshore spawning: Diel patterns

L. reynaudii is an intermittent terminal spawner with an estimated female fecundity of 8 000-17 000 eggs (Melo and Sauer 1999, Sauer et al. 1999, Rocha et al. 2001). The mating system is complex as it comprises, *inter alia*, of agonistic courtship rituals involving fighting – guarding by small sneaker and, or large consort males over 'egg beds', with a male:female ratio of ~2:1 on inshore spawning grounds (Augustyn 1990, Hanlon et al. 2002, Downey et al. 2010). This results in potentially multiple paternities within an egg capsule, also called a string or strand, following non-random and potentially active female agency in which stored spermatophores are used in fertilisation (Shaw and Sauer 2004, Naud et al. 2016). Females deposit gelatinous egg capsules (strings) in clusters with capsules containing in the region of 110 ± 16 eggs (Augustyn 1989, Augustyn et al. 1994). Masses of capsules are attached by their basal stalks to form 'egg beds' up to 4 m in diameter, mostly within substrates of sand – low-lying reef. This inshore process of mating and egg deposition occurs in the vicinity of spawning aggregations (Sauer et al. 1992, Sauer et al. 1997, Hanlon et al. 2002).

Squid aggregate to spawn on the Plettenberg Bay-Port Alfred inshore area throughout the year, presumably with a greater and lesser peak around September-December (spring-summer) and March-July (autumn-winter) respectively (Augustyn et al. 1994, Githaiga-Mwicigi 2023). The seasonal prevalence and intensity of these aggregations are interlinked with the presence of optimal spawning conditions, shown to vary and change according to the strength of seasonal summer Easterly (upwelling) or winter Westerly (swell-inducing) winds, in relation to mesoscale physical oceanography which partly results from teleconnections with the El Niño Southern Oscillation (Roberts and Sauer 1994, Schön et al. 2002, Sauer et al. 2013). Such environmental variability also influences the interspecific and intraspecific dynamics in the day-to-day incidence of reproduction at known ‘marks’ of spawning sites (Downey et al. 2010).

Virgin inshore spawning sites may be first seeded with egg depositions *in situ* of aggregations involving suprabenthic mating and benthic ovipositioning (Sauer et al. 1992, Downey et al. 2010). Aggregations are seemingly induced by mild upwelling and, once established, largely alternate between states of diurnal courtship, copulation and, or oviposition activity, and nocturnal resting, feeding and, or oviposition activity at a moderate flux of 11.5–19.6°C (Sauer and Lipiński 1991, Sauer et al. 1992, Sauer et al. 1997, Downey et al. 2010). However, the persistence of aggregations depends, in part, on the continuity of conditions conducive to spawning. Spawning activity and, or aggregate behaviour typically ceases when the sea state becomes too turbulent, too turbid, and, or there is a sharp decline in temperature with sudden major upwelling (Roberts and Sauer 1994, Downey et al. 2010). Where and when local conditions are favourable, seeded sites arguably serve as ‘homing beacons’ for mature squid to start or continue their serial spawning (Downey et al. 2010, Martins et al. 2014).

Spawning individuals can travel ~200 km in 18 days (~3.07 km/day) on their inshore reproductive grounds (Sauer et al. 2000), although the exact duration of pre-senescent monocyclic spawning seems to currently remain unclear. Such travel can involve diurnal and, or nocturnal migration between spawning sites (Sauer et al. 2000, Downey et al. 2010); mainly diurnal spawning (i.e., suprabenthic mating and benthic ovipositioning); occasional nocturnal spawning (i.e., suprabenthic mating and, or benthic ovipositioning) (Sauer et al. 1992, Sauer 1995, Sauer et al. 1997, Downey et al. 2010); dispersive nocturnal feeding offshore or at spawning sites (Sauer and Lipiński 1991, Sauer et al. 1997, Downey et al. 2010); and, or dispersive diurnal – nocturnal resting offshore or proximate to mating arenas, when breaking from active spawning (Sauer et al. 1997, Downey et al. 2010). However, despite fine-grained variability in individuals' inshore diel spawning behaviour, there remains an overarching pattern of day-to-night decreases in the concentration of aggregations. Male-female spawning typically ceases around dusk and a marked portion of individuals emigrate to rest, feed and, or continue in their spawning migrations. And old spawners return – new spawners arrive, immigrating onto a viable spawning mark typically around dawn. This shows a mostly persistent presence of an aggregation core as long as sites' spawning conditions continue to be conducive (Downey et al. 2010). Also, this pattern seems to allude to changes in local abundance and regional distribution and, by association, any catches made within and between nighttime and daytime periods (Downey et al. 2010, Bochenek and Powell 2021).

1.3.3 Commercial fishery and importance

Locally known as chokka, *L. reynaudii* has been harvested in a commercial squid fishery on the South African southeast coast since 1982 (Augustyn et al. 1992). Targeted commercial harvesting[6] started with small-boat business ventures (Augustyn, 1986 cited in Augustyn and Roel 1998, p. 71), where relatively small complements of crew used handline jigging to harvest squid for sale on local to international markets (Augustyn et al. 1992, Augustyn and Roel 1998). Today, 'chokka boats', ~20m deck-and-freezer vessels can accommodate larger complements of crew when going to sea for ~21 days at a time during the season open for fishing. These vessels target squid on or close to aggregate spawning grounds found at <50m water depth, mainly between Plettenberg Bay and Port Alfred (Githaiga-Mwicigi 2023). Once aggregations have been located, chokka boats deploy chained anchor/s to maintain position while fishing (Githaiga-Mwicigi 2023). Fishing crew employ handline jigging, often operating two lines at a time to fish during daylight hours. When fishing in deeper waters, where deployment of anchors on chain is not practical, vessels try to hold position using a drogue.

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[6] Chokka has been taken as demersal trawl bycatch from before 1980, of which recent annual harvests have ranged between 200 and 800 tons (DEFF 2020, DFFE 2023).

When fishing after sunset, vessels mimic daylight by way of artificial, 1-2kw boat-based lighting (Sauer 1995, Githaiga-Mwicigi 2023).

The commercial squid handline jigging fishery is considered the third most lucrative in South Africa, generating >R480 million in annual revenue when catches are good (DEFF 2020, DFFE 2023). However, interannual catches of adult chokka tend to have a high degree of variability (See Figure 4; Githaiga and Louw 2024) and change, in part, according to the prevalence, frequency and intensity of spawning aggregations, consequent to the favourability-unfavorability of spawning conditions (This study). This leads to relevant fisheries management requiring a fine balance between the ecological sustainability of the squid fishing stock (Rodhouse et al. 2014) and socio-economic security of the ~3000 fishery-related employees mostly residing locally in the Eastern Cape (Downey et al. 2010, DEFF 2020, DFFE 2023).

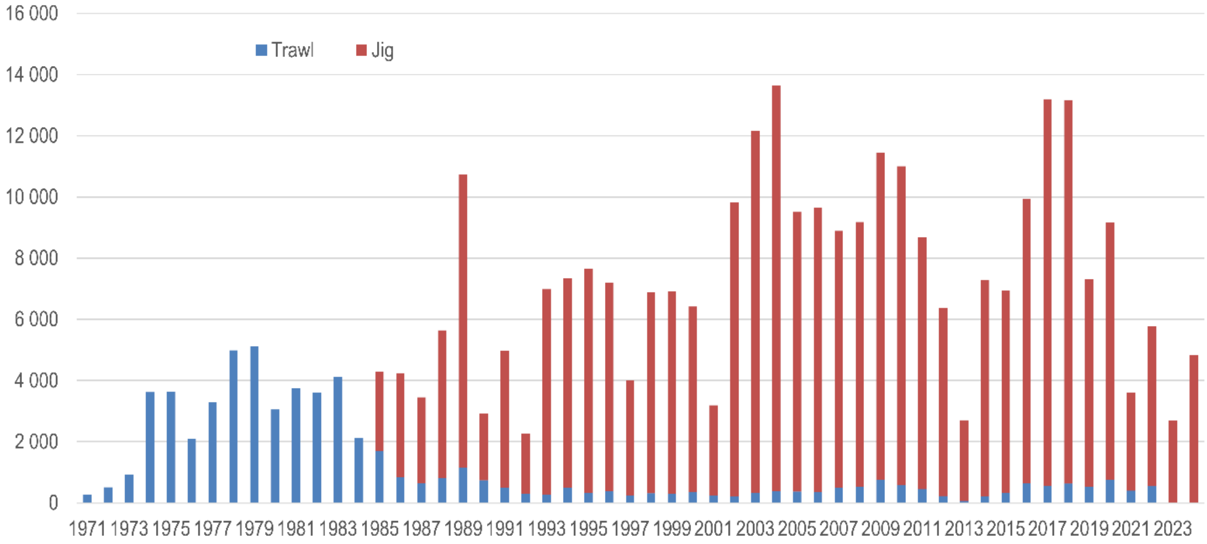

Figure 4: Annual metric tons of *L. reynaudii* landed as bycatch in the demersal trawl fishery and targeted catch in the commercial squid jig fishery of South Africa (Githaiga and Louw 2024).

1.3.4 Stock assessment and management

The current primary objective of the Fisheries Management Branch of the Department of Forestry, Fisheries and the Environment of South Africa (DFFE:FB), in managing the chokka squid jig fishery, is to achieve the greatest possible, average long-term catch while not risking reductions in the stock biomass to levels where long-term recruitment of the stock is compromised by excessive exploitation (DEFF 2020, DFFE 2023).

Managing the stock and associated fishery has progressed from largely common-sense measures (e.g., award of limited number of permits and periodic closure of the fishery to harvesting) (Augustyn et al. 1992, Augustyn and Roel 1998) to also a full stock-assessment where projections of stock status, under differing levels of jigging effort expended, are evaluated (Roel 1998, Sauer et al. 2013, Glazer 2019). A stock assessment was first carried out in 1998 to estimate the risk of stock collapse (i.e., a <20% spawner biomass in ≥1 year, as compared to average 'pristine' pre-exploitation levels) under the fixed level of the then 3.6 million man-hours in annual jigging effort. Employing squid jig catch per unit effort (CPUE), standardised trawl CPUE and autumn-spring DFFE hake-directed, swept-area biomass survey data, a biomass-dynamic model with observation-error was used to carry out 10-year recruitment biomass projections for periods of January to March and April to December (Roel 1998, Roel and Butterworth 2000, Sauer et al. 2013). Some of the assumptions of the assessment model included: a constant recruitment at >20% pre-exploitation spawner biomass levels, linear decline in recruitment at less-than-pristine biomass levels, and decreases in spawning activity and spawner survival (i.e., recruitment success) with increases in jig fishing pressures. Findings indicated a ~90% risk of stock collapse and researcher recommendations included a ~33% (~1.188 million man-hour) decrease in jigging effort, barring national-level socio-economic concerns (Roel 1998, Roel and Butterworth 2000, Sauer et al. 2013).

A subsequent 6-year absence of the squid stock's collapse under continued annual effort levels of ~3 million man-hours, led Glazer and Butterworth (2006) to refine initial assessment procedures. Updates included additional incorporation of process-error estimators and use of a Beverton-Holt rather than 'hockey-stick' stock-recruitment relationship. Findings included a less severe, ~80% risk of stock collapse with ~4 million man-hours in annual jigging effort (Glazer and Butterworth 2006). Most recently, the 2019 assessment used a Baranov model employing jig and trawl landings, nominal jig and standardised trawl CPUE, and autumn and spring biomass survey data to estimate person-day effort levels at which there is a >5% probability of a <20%, sub-pristine spawner biomass in ≥1 year over a of 10-year period.

Findings indicated that it was safe to increase annual effort levels from 270,000 to 295,000 person-days (Glazer 2019).

At present, DFFE:FB manages the fishery by way of a 12-month Total Allowable Effort (TAE) of 295,000 person days, accounted for by 2,443 fishing crew operating per fishing season between May and April. On completion of DFFE's 2021/2022 Fisheries Rights Allocation Process (FRAP2021/22), the global TAE (295,000 person-days) was divided into 44,250 person-days (366 crew) for Small-scale and 250,750 person-days (2,077 crew) for Commercial effort expenditure (DFFE 2023, Githaiga-Mwicigi 2023). Management also currently involves the implementation of two closed seasons (Durholtz and Glazer 2022, Githaiga-Mwicigi 2023). Harvesting has been prohibited for 5 weeks, from 19 October to 23 November by Government Gazette, since 1993. This serves to optimise reproductive success during the peak spawning period in October-November. Since 2014, there has also been consensus between industry and government on an additional closed season of up to 3 months, around April to June (autumn-winter). This is to ensure the annual TAE is not exceeded (Durholtz and Glazer 2022, Githaiga-Mwicigi 2023, DFFE 2023). While the gazetted spring closure is fixed, the agreed-on autumn-winter closure may be started earlier or later depending on how fast or slow the fishery is, in reaching the prescribed TAE. For example, the standard autumn-winter closed season is from 1 April to 30 June, but the actual 3-month 2015 closure was from 1 March to 31 May and, in 2022 and 2023, autumn-winter closure was only for two months from 1 May to 30 June (Durholtz and Glazer 2022, Githaiga-Mwicigi 2023).

1.4 Problem statement

There is a present need to assess long-term spatial-temporal variations in the population of adult chokka and related fishing pressures on the commercial squid jig fishing grounds of South Africa (Githaiga-Mwicigi, 2023). The current South African squid Fishery Stock Assessment Model (FSAM) assumes recruitment occurs once per year during January (Durholtz and Glazer 2022), irrespective of any actual intra-inter annual variations in recruitment with the occurrence of seasonal peaks in annual spawning (Augustyn et al. 1994). Along with findings that chokka tend to spawn when close to but younger than one year old (Lipiński et al. 2020), assumptions of senescence at ~13 months and allocation of 15% of the TAE to small-scale fishers in recent years (Durholtz and Glazer 2022), limitations in the current model have led to a panel of International Experts recruited by the University of Cape Town's

Marine Resource Assessment and Management Group (MARAM), recommending, at the 2022 annual International Stock Assessment Workshop, a review of the current squid FSAM (Githaiga-Mwicigi 2023). These developments in research and management have led to calls within DFFE's Squid Scientific Working Group (Squid SWG) for the assessment of diel changes in chokka catch within and between seasons and years, especially to augment relevant hydroacoustic survey findings and design (This study, Githaiga-Mwicigi 2023, Hampton 2023, Hampton et al. 2024).

Hydroacoustic surveys have been developed and deployed in recent years to standardise another form of regular scientific inquiry into chokka biomass, reproductive output and abundance (Durholtz and Glazer 2022, Hampton et al. 2022, Hampton et al. 2024). Surveys were conducted on the commercial chokka fishing grounds during daylight hours in the November 'closed season' of 2019-2022, when squid form aggregations which are detectable using these methods (Hampton et al. 2022, Soule and Hampton 2022).

Hydroacoustic surveys were in the form of grid transects over waters ≤50 m deep, piloted over part of the fishing grounds using the *Ellen Khuzwayo* (a 43.2 m DFFE research vessel) in 2019 and *Abyss* (a 7.5 m rigid-hulled DFFE research inflatable) in 2020. In 2021 and 2022, surveys were carried out over the whole main fishing grounds through a combination of efforts made using both aforementioned vessels. These surveys seemed to provide biomass estimates which reasonably corresponded with total commercial catch landed in the weeks to months following their conclusion (Hampton et al. 2022, Soule and Hampton 2022, Hampton et al. 2024). However, Soule and Hampton (2022) highlighted it was still uncertain how applicable these acoustic estimates were as absolute or relative measures of the adult population as a whole. This was due to postulations that a considerable proportion of the October-November squid population may be too dispersed at daytime for hydroacoustic detection, despite indications that chokka mostly aggregate and spawn at daytime. Alternatively or concomitantly, it may have been the case that, within a survey period, squids were mostly located outside the spatial range to which surveys were carried out (e.g., at >50 m depths – outside the main fishing/spawning grounds) (Hampton et al. 2022, Soule and Hampton 2022, Githaiga-Mwicigi 2023, Hampton et al. 2024).

As a potential remedy, Soule and Hampton (2022) recommended investigating how diel-type differences in catch rates vary seasonally on the commercial fishing grounds throughout the year, considering: commercial vessels operate over a longer period throughout the year; squid may be jigged without restriction per 24 hour period; jigging sessions may be carried out within and beyond acoustic survey spatial borders; and commercial catches and catch rates largely depend on the prevalence, duration and intensity of chokka aggregations (Githaiga-Mwicigi 2023). And Hampton et al. (2022) recommended, *inter alia*, for a perspective of squid population dynamics which is temporally broader than achieved through annual 'closed-season' surveys so far. The premise is that such research would help in better ascertaining the aggregate proportion of the chokka population. Thus, such research would, *inter alia*, help determine how acoustic survey findings can apply as absolute or relative measures of the adult chokka population as a whole, and provide a perspective of the said population's abundance and distribution dynamics which is temporally more holistic. Since chokka can only be surveyed acoustically when aggregated, such research would also help optimise acoustic survey design in terms of when and where future sampling is carried out (Hampton et al. 2022, Soule and Hampton 2022, Hampton 2023).

1.5 Project aim & objectives

The purpose of this study was to investigate diel changes in *L. reynaudii* (chokka) catch rates and chokka behaviour on the commercial squid jig fishing grounds of South Africa (See Figure 5). The project aimed to achieve this through a statistical model-based approach using DFFE session-level squid jig catch logbook data in estimating diurnal-nocturnal variations in chokka Catch Per Unit Effort (CPUE). Such an approach was deemed necessary as *standardised* CPUE was assumed to be a representative measure of local chokka abundance and proportional representation of regional population distribution.

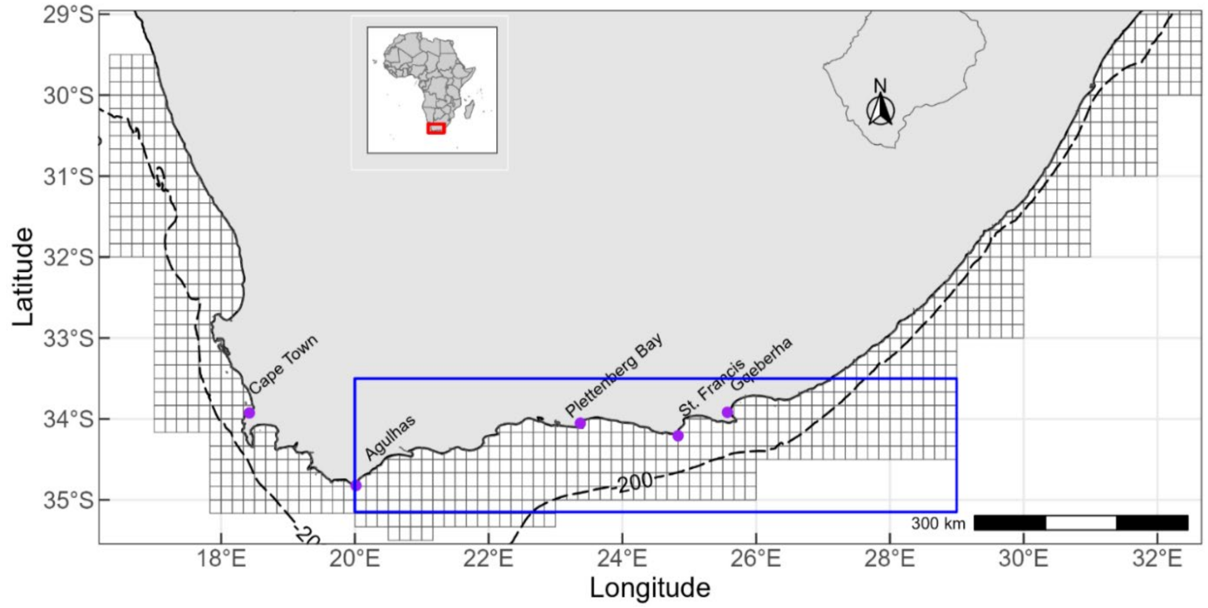

Figure 5: The commercial squid jig fishing grounds of South Africa as defined by the DFFE:FB fishing grid cell ‘squid grid’. The blue rectangle denotes 20-29°E, covering the arguable areal core of relevant fishing activity and to which model-based analyses were spatially limited with this investigation.

Modelling was therefore carried out to investigate whether there are any differences in patterns of catch rates and, hence, chokka behaviour during day vs night and, further, whether such fishing and ‘fish’ behaviour patterns are influenced by effects of space and temporal parameters such as season. Accordingly, study research questions were:

1. Is there an effect of diel period on chokka CPUE on the commercial squid jig fishing grounds of South Africa?
2. Is there seasonal variation in any effects of diel period on chokka CPUE on the commercial squid jig fishing grounds of South Africa?
3. Is there spatial variation in any effects of diel period on chokka CPUE between seasons and years on the commercial squid jig fishing grounds of South Africa?

Chapter 2: Methods

An iterative semi-inductive approach was primarily taken to estimate chokka CPUE as a function of relevant space-time variables. In answering project research questions, such an approach allowed for the employment of ampliative reasoning in the refinement and potential change of estimated parameters (Mentis 1988).

All data-related procedures and processes were carried out in the R Statistical Environment for Scientific Computing (Version 4.3.2; R Core Team 2023) using the widely used Integrated Development Environment RStudio (Version 2023.12.1+402; Posit team 2024). This allowed for appropriate preparation and relevant exploration of the data followed by modelling and model-based inferences. For example, multiple R packages were used for data exploration, modelling, checking model diagnostics, and finally processing and summarising model outputs. These included: *tidyverse* (Version 2.0.0; Wickham et al. 2019), *sf* (Version 1.0.16; Pebesma 2018, Pebesma and Bivand 2023), *rworldmap* (Version 1.3.8; South 2011), *rworldxtra* (Version 1.1; South 2012), *ggspatial* (Version 1.1.9; Dunnington 2023), *rnaturalearth* (Version 1.0.1; Massicotte and South 2023), *rnaturalearthhires* (Version 1.0.0.9000; South et al. 2024) and *metR* (Version 0.15.0; Campitelli 2021) packages. Also, bathymetric contour data was sourced from the NOAA National Centers for Environmental Information (NOAA National Centers for Environmental Information 2022) using the *getNOAA.bathy* function in the *marmap* package (Version 1.0.10; Pante et al. 2023). And relevant town and city locations were plotted using data adapted from Strauss (2017).

2.1 The data

Commercial squid jig catch data was acquired from DFFE:FB on 7 December 2023 in the form of a *.sqlite* database, later queried to extract all the required data sets.

Under the direction of DFFE:FB, permit conditions require chokka boat skippers to use a DFFE issued standard format catch logbook to record the Date, Number of fishing crew, Start and End time of fishing, fishing session Latitude and Longitude, fishing Depth, whether eggs were present, number of attempts to deploy one anchor A, or a second anchor B, and the total kilograms of squid caught at the end of a fishing session (Githaiga-Mwicigi 2023). Upon completion of a fishing voyage, these data are submitted to DFFE:FB along with details of the relevant fishing vessel, vessel skipper, permit rights holder and intended processing plant. DFFE:FB staff then enter these data into a Microsoft Access database to compile records into a table format (Githaiga-Mwicigi 2023). Hence, these data provided information on individual chokka boats' geospatial coordinate details (e.g., point Longitude-Latitude and, or Fishing grid cell number), sonar-based bathymetry, time of fishing, catch made and effort expended per jigging session, with each voyage. CPUE was thus defined as the average kilograms caught per fisher minute expended per jigging session, calculated as

$$CPUE_g = \frac{kG_g}{\left(p_g \times d_g\right)} \tag{2.1}$$

where:

$CPUE_g =$ CPUE calculated for jigging session g;

$g = i^{th}$ fishing session;'

$kG =$ total weight caught;

$p =$ total number of people who fished; and

$d =$ total minute duration.

2.2 Data preparation

As noted above raw data was provided as a *.sqlite* database, accessed in R using the *RSQLite* (Version 2.3.6; Müller et al. 2024) *DBI* (Version 1.2.2; R Special Interest Group on Databases (R-SIG-DB) et al. 2024). General data manipulation was done using sets of R packages that make up the *tidyverse* (Version 2.0.0; Wickham et al. 2019), and the *clock* (Version 0.7.0; Vaughan 2023) package for processing date-time objects. The total number of raw data comprised about 390,650 records. *Inter alia*, data rows were filtered to comprise of complete cases of 2006-2022 jigging sessions, recorded to have been carried out in water > 5 meters or ≤ 300 meters deep; outside periods known to have been historically closed for commercial jigging operations (See Chapter 1); and within areal bounds of the South African commercial squid jig fishing grid as defined by DFFE (See Figure 5). These data processing procedures were carried out to exclude records with an arguably high risk of being erroneous or erroneously recorded. For example, commercial squid jig harvests have been recorded using relatively detailed logbooks, specific to the chokka jig fishery, only since 2006 (DEFF 2020, DFFE 2023). And, when third-party data was received from DFFE, relevant records were considered the most complete and accurate up to end of 2022. About 44,950 rows were excluded following the above noted data quality control and inclusion rules, leading to preliminarily cleaned data comprising a sample size of 345,700 jigging sessions.

Data preparation also involved using the *getSunlightTimes* function from the R *suncalc* package (Version 0.5.1; Thieurmel and Elmarhraoui 2022) to classify session start and end date-times to diel periods. This enabled consecutive classification of sessions' start and end date-time to diel periods as:

- dusk when ≥ "sunset" and ≤ "night";
- dawn when ≥ "nightEnd" and ≤ "sunrise";
- day when ≥ "sunrise" and ≤ "sunset";
- night when ≥ "night" and ≤ 23:59:59; and
- night when ≥ 00:00:00 and ≤ "nightEnd" (Thieurmel and Elmarhraoui 2022).

In addition, preliminarily cleaned data were further checked for outliers and observations identified as outliers were excluded. Outlier detection employed the medcouple-based approach from Hubert and Vandervieren (2008)[7]. At this study's relevant stage of data handling, the response's medcouple was calculated to be ~0.39 using the *mc* function from the *robustbase* package (Version 0.99-2; Maechler et al. 2024). As this value was ≥ 0 and ≤ 0.6 (Hubert and Vandervieren 2008), observations were classified as outliers using the *boxB(…, method = "adjbox")* function from the *univOutl* package (Version 0.4; D'Orazio 2022), to identify observations as outliers when outside the interval

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[7] The medcouple can be described as a measure of univariate departure from a symmetric probability distribution, bounded between -1 and 1 (Brys et al. 2004, whuber 2022). In cases where the medcouple was ≥ -0.6 and ≤ 0.6, Hubert and Vandervieren (2008) were fairly successful in employing this measure in identifying 'outliers', values arguably unlikely to be actual, non-erroneous, extremely low or extremely high observations given the data's potentially skewed probability distribution.

$$[Q_1 - 1.5 \times e^{-4 \times \mathrm{MC}} \times IQR;\ \mathrm{Q}_3 + 1.5 \times e^{3 \times \mathrm{MC}} \times IQR] \qquad (2.2)$$

where:

Q_i denotes the i$^{\text{th}}$ quartile;

IQR denotes the Inter Quartile Range;

e denotes the exponent; and

MC denotes the medcouple (Hubert and Vandervieren 2008, D'Orazio 2022).

Outlier detection procedures led to the exclusion of 4,652 rows of data, resulting in a final to-be-explored sample size of 341,048 jigging sessions.

2.3 Data exploration

Multiple R packages were employed in data exploration including the: *tidyverse* (Version 2.0.0; Wickham et al. 2019), *janitor* (Version 2.2.0; Firke 2023), *ggh4x* (Version 0.2.8; van den Brand 2024), *sf* (Version 1.0.16; Pebesma 2018, Pebesma and Bivand 2023), *rworldmap* (Version 1.3.8; South 2011), *rworldxtra* (Version 1.1; South 2012), *ggspatial* (Version 1.1.9; Dunnington 2023)*, rnaturalearth* (Version 1.0.1; Massicotte and South 2023), *rnaturalearthhires* (Version 1.0.0.9000; South et al. 2024), *metR* (Version 0.15.0; Campitelli 2021) and *colourpicker* (Version 1.3.0; Attali 2023) packages. *Inter alia*, exploratory analyses served to inform student-supervisor deliberations and agreement, and lead to modification of the modelling approach and corresponding data used. For example, the data used were limited to sessions carried out purely at day or night between 20-29°E (See Figure 5), over a maximum length of ≤ 481 minutes (~8 hours), comprising a sample size of 136,840 jigging sessions.

2.4 Modelling

2.4.1 Generalized Additive Models (GAMs)

Non-linearity is commonly observed in most ecological relationships. Thus, it was decided to consider a modelling frame-work that naturally allows for modelling non-linear effects. To this end, Generalized Additive modelling was adopted.

Generalized Additive Models (GAMs) allow for the exploration and estimation of 'wiggly' response-predictor relationships by way of penalised splines, also called ‘smooths’ (Hastie and Tibshirani 1986, Hastie and Tibshirani 1987, Wood 2017). These types of models are therefore useful in ecological studies but also have fisheries applications. Examples include the standardisation of CPUE, where it is arguably not a rarity for relevant data to be complex non-linear – non-normal (Hoyle et al. 2024). This was also the case with the data for this project, which incentivised consideration of semi to non-parametric approaches to modelling chokka CPUE. In addition to gaussian distributions, generalized additive modelling also allows researchers to consider one of the multiple exponential family of distributions such as a *tweedie*. Another advantage of a GAM (but also a Generalized Linear Model, i.e., GLM), over standard linear regression, is the ability to specify link-functions whereby actual model fitting can be done in the link space. This allows for modelling various types of response variables including a binary response using a logit or probit link, count data using a log-link, or, if one chooses so, symmetrically distributed data using an identity link (Zuur et al. 2009, Wood 2017).

For the purposes of this study, a Generalized Additive Model (GAM) was applied following a *tweedie* distribution with a log-link function, using the *mgcv* package (Version 1.9.1; Wood 2003, Wood 2011, Wood et al. 2016, Wood 2017).

The *tweedie* distribution (Tw) forms part of the exponential family of probability distributions, characterised by a mean-variance relationship which can be specified as

$$V(\mu) = \mu^{p} \tag{2.3}$$

where:

$V()$ denotes the variance function;

μ denotes the population mean; and

p denotes an unknown (θ) power parameter (Dunn and Smyth 2005, Wood et al. 2016).

Hence, Tw arguably also constitutes a family of distributions as it is potentially equivalent to the form of, *inter alia*, a Gaussian (p = 0), Poisson (p = 1) or Gamma (p = 2) probability (Dunn and Smyth 2005, Wood et al. 2016). *mgcv* allows for Tw model approximations where 1 < p <

2. This can be achieved by setting the family argument to “Tweedie” in a call to any of the *mgcv* modelling engines but requires specifying a value for p *a priori*. Alternatively, *mgcv*’s *gam* and *bam* functions also allow setting the family argument to “tw”, for p to be estimated during model fitting (Wood et al. 2016, Wood 2017). Further, in specifying an *mgcv* GAM as a *bam* or *gam*, additional options include the potential consideration of smooth-type (depending on the type of variable, one can specify different types of smoothers) and specifying random effects structures when formulating and selecting among candidate models (Wood 2017, Simpson 2021).

Multiple mixed-effect models were considered for the purpose of this study. These models comprise of both fixed and random effects. “Fixed” effects pertain to terms’ mean effect relative to a ‘global’ intercept (simple regression) or baseline intercept (multiple regression). On the other hand, “random” effects account, *inter alia*, for potential group-level variations in the slope and, or intercept of predictor’s relation to the response. As a result, mixed effect models potentially involve controlling for ‘random’ variation due to nuisance variables, when making inferences regarding the predictor effects which are of main study interest (Gelman 2005, Gelman and Hill 2007, Wood 2017). Such control and inference are possible with *mgcv* by additionally specifying random effect smooth terms in the form of *s(…, bs = ‘re’)* when using *bam* (or *gam*) models (Wood et al. 2015, Wood 2017, Simpson 2021).

R’s *mgcv bam* was conceptualised to optimally minimise software computation time and memory load when required model matrices are considerably large to build in-memory. In the case of non-Gaussian GAMs, optimisation is achieved by employing an adaptation of the Penalised Iteratively Reweighted Least Squares (PIRLS) algorithm. This involves first generating estimates of necessary starting values by fitting the specified model to a subsample of the data. Starting values are then employed in piecewise estimation and update of the relevant model matrix’s QR decomposition, ultimately allowing for efficient modelling of data comprising upwards of tens of thousands of observations (Wood et al. 2015, Wood 2017). It was therefore deemed appropriate to broadly specify project candidate models as *bam(…, family = tw(link = “log”)* considering the Gamma-type structure of the response’s empirical probability distribution (See Figure 6) and that the data comprised of 136,840 observations. This formed part of an iterative process of selection and estimation to optimally describe relevant variables' effect on the response (Zuur et al. 2009, Wood et al. 2015, Wood et al. 2016, Wood 2017).

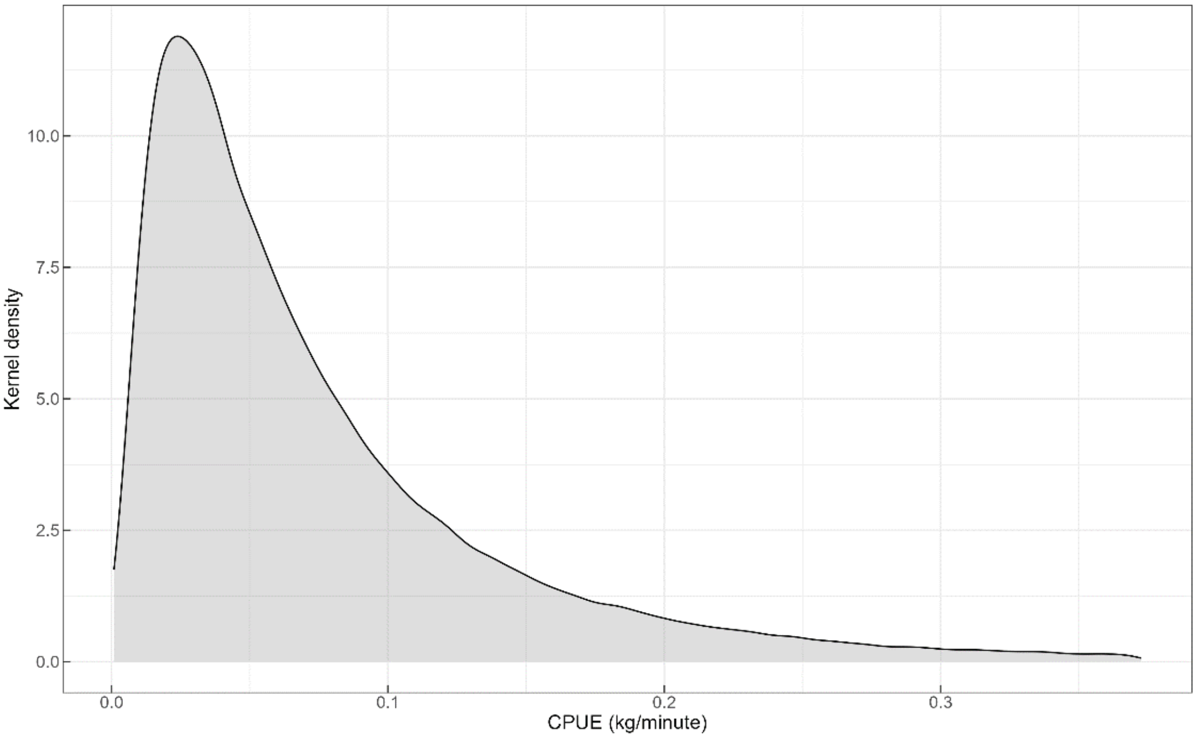

Figure 6: Empirical probability distribution of nominal CPUE in the modelling data.

2.4.2 Model selection-refinement-validation

Model selection involved 10 repetitions of hold-out Cross Validation (CV) to estimate a mean of candidate models’ Root Mean Square of Prediction Error (RMSPE)[8] (Kim 2009, Hodson 2022). CV is an established method of model selection as it allows evaluation of a model’s ability to estimate the response according to out-of-sample predictor values. In fisheries research, this arguably leads to selection of a model which strikes a relatively optimal balance between fitting the in-sample data and describing the underlying phenomenon of interest at a population scale (Stone 1974, Browne 2000, King et al. 2021, Hoyle et al. 2024). And while

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[8] As an error metric, RMSPE has the advantage of being on the same scale and thus directly comparable to the relevant response. This makes interpreting the predictive power of a model relatively simple (Hodson 2022).

CV includes the k-fold and Leave-One-Out method, repeated hold-out CV was deemed to have fairly adequate analytic statistical power while not being overly demanding in terms of computational feasibility (Stone 1974, Kohavi 1995, Kim 2009, Hoyle et al. 2024). Hence, with each repetition of hold-out CV, 70% of the data was randomly sampled without replacement and used to train each of the candidate models before predicting the held-out 30% and calculating RMSPE as

$$RMSPE = \sqrt{\frac{1}{n}\sum_{i=1}^{n}(y_i - \hat{y}_i)^2} \qquad (2.4)$$

where:

n denotes a sample size of $(i = 1, 2, \dots, n)$ for $y(y_i)$ and $\hat{y}(\hat{y}_i)$,

y_i denotes the i^{th} response value observed in the CV hold-out set, and

$\hat{y}_i$ denotes the i^{th} response value predicted according to corresponding predictor values in the CV hold-out set (Hodson 2022).

This allowed for objective selection among candidate models according to their estimated predictive accuracy.

The final selected model was applied to the full data set for refinement, diagnostic, validation and interpretation procedures (Wood 2003, Wood 2011, Wood et al. 2016, Wood 2017). Refinement involved using *mgcv*'s *k.check* function to iteratively assess the number of basis functions (*k'*) per smooth term, and adjust associated basis dimensions (*k*) accordingly if possible and deemed necessary (Wood 2017). Basis dimensions (*k*) affect the degree of nonlinearity allowed for in model estimates as they determine *k-1*, the maximum possible number of *k'* basis functions computed per smooth term. Hence, to allow for an appropriate degree of nonlinearity, relevant terms' *k* was doubled before refitting the model, until *k.check* showed a >10 *k′* vs Effective Degrees of Freedom (EDF) difference and ≥0.05 p-value[9] for each non-random effect smooth. And, considering *k.check* did not compute a p-value for random effect smooths potentially included in the model, relevant terms' *k* was doubled before refitting the model, until *k.check* showed a >10 *k′* vs EDF difference for each random effect smooth (Wood 2017). However, these non-linearity adjustments could not be applied for every term. For example, modelling involved 17 years of data and *k* could thus only be increased up to 17 in the univariate thin-plate regression smooth term for "year". These refinement protocols were followed to ensure an optimal fit to the data prior to carrying out any final model diagnostics – validations (Wood 2003, Wood 2011, Wood et al. 2016, Wood 2017).

Model fit was evaluated to ensure method assumptions were satisfied to an arguably adequate degree. Following Wood et al. (2016) and Wood (2017), GAM models, using a *tweedie* distribution, at least assume:

1. **The response follows a theoretical *tweedie* distribution of the form $1 < p < 2$, as specified by the model in question**. This was inspected by way of the p value estimated as part of model fitting in R (Wood 2017, Wood 2023); and a quantile-quantile plot constructed using the *gratia* package's *qq_plot(…, method = "simulate")* function (Version 0.9.0; Simpson 2024), where deviance residuals were plotted against simulated theoretical quantiles (n = 50) (Augustin et al. 2012).
2. **Error terms are normally distributed**. Deviance residuals were extracted from the model using the *gratia* package's *add_residuals* function (Version 0.9.0; Simpson 2024) and assessed for distributional normality through construction of a residual frequency density plot (Wickham et al. 2019).
3. **Deviance residuals are homoscedastic**. A Linear predictor vs Deviance residuals plot was constructed using the *gratia* package's *residuals_linpred_plot* function (Version 0.9.0; Simpson 2024), to assess whether residuals deviated randomly around zero.

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[9] Per term, *k.check* p-values result from testing the H_0 that *k* has been set high enough for modelling procedures to completely describe patterns in the data (Wood 2017, Wood 2023).

Additionally, extracted deviance residuals were plotted against jigging sessions' reported water depth and total minute duration, per diel period, to check whether there were any relevant patterns remaining in the data, unaccounted for by the model.

4. **Observations are independent**. There is a need to check for spatio-temporal independence of residuals, as the model assumes that no spatial and temporal autocorrelation remain in the residuals after accounting for the effect of all the variables included in the model (Hurlbert 1984, Legendre 1993, Hoyle et al. 2024). The final model was therefore tested for residual autocorrelation using the *testTemporalAutocorrelation* and *testSpatialAutocorrelation* functions in the *DHARMa* package (Version 0.4.6; Hartig 2022), grouping by Year with the former and Fishing grid cell with the latter. Further, extracted deviance residuals were plotted by year and month per diel period to visually inspect for any spatial-temporal patterns (Wickham et al. 2019).
5. **Terms are not overly concurve**. Concurvity is a nonlinear extension of multicollinearity since, in a model with concurvity, colinear terms are non-independent and thus have a 'shared' effect in their relation to the response. This leads to modelling procedures not providing stable estimates of covariates' partial effect as there can be no clear separation in the variation explained by these predictors. Hence, highly concurve terms may be redundant and, or lead to fluxes in model estimates with minor variations in colinear predictor values. A model may therefore arguably require reassessment to exclude concurve terms from its formulation (Buja et al. 1989, Graham 2003, Ramsay et al. 2003, Pedersen et al. 2019, Siems et al. 2023). However, parametric-type concurvity is arguably unavoidable and non-problematic when involving terms with relatively few factor levels (Simpson 2022). These aspects were evaluated using the *gratia* package's *concrvity* function (Version 0.9.0; Simpson 2024), to assess the final selected model's overall and smooth-based pairwise concurvity. *concrvity* produces three metrics, termed "worst", "observed" and "estimate", ranging from 0 (no concurvity) to 1 (perfect concurvity). However, these metrics also differ in that "estimate" is arguably a relatively more realistic measure while "worst" tends to overestimate and "observed" potentially

underestimates any concurvity of model terms (Wood 2023). Hence, this study mostly focussed on the “estimate” metric when evaluating model terms’ concurvity.

6. **Random effect approximations follow an independent and identically distributed Gaussian probability**. Using the *gratia* package’s *draw* function (Version 0.9.0; Simpson 2024), any random effect smooth terms’ partial effects were plotted against modelled Gaussian quantiles.
7. **Model fitted values positively correspond with the observed response**. Fitted values were extracted from the model using the *gratia* package’s *add_fitted* function (Version 0.9.0; Simpson 2024) and plotted against observed data values using the *gratia* package’s *observed_fitted_plot* function (Version 0.9.0; Simpson 2024) and by way of a scatterplot (Wickham et al. 2019). This allowed for visual assessment of Fitted-Response value correspondence overall and per year. Additionally, extracted deviance residuals were boxplotted to assess fitted value accuracy in estimating observed response values, according to year and month per diel period (Wickham et al. 2019).

Posterior Predictive Checks (PPCs) were carried out as a final step in validating the selected model’s specification. PPCs involve simulating multiple sets of the response according to the predictive distribution specified by the model *a posteriori* of fitting to empirical data. This allows for a check on how accurate the model is in estimating actual response values. In other words, PPCs allow discerning whether model parameters require changes – further refinement to better describe the observed data (Gabry et al. 2019). In this project, such posterior predictive ‘draws’ were generated and plotted using relevant functions adapted from Santon et al. (2023), to visually screen for gross differences between actual observed values and model descriptions of the data.

2.4.3 Model interpretation

Research questions were addressed by assessing the direction and magnitude of the effect for parametric terms and by evaluating smooth terms’ partial effects (marginal effects of terms at the mean of continuous variables and first level of factors when not specifically chosen/specified by the user). Model terms’ estimated effect on the response was inferred to be statistically significant (i.e., high enough chance for terms’ effect to be non-zero) when shown to have a p-value of <0.05 in the model summary (Wood 2013, Wood 2017).

2.5 Results: Method details summary

Chapters 3, 4 and 5 pertain to results following exploration of the filtered-cleaned catch records, implementation of model selection-refinement-validation procedures and estimation of relevant model terms' marginal effects, respectively:

- Chapter 3 provides a spatial-temporal overview of the 2006-2022 South African commercial squid jig fishery, with figures illustrating data trends/patterns specific to (1) association between the total number of sessions and total kilograms caught per year; (2) sessions' proportionate per month per year frequency within and, or between diel periods; (3) total kilograms caught and sessions' average hourly duration per year; (4) where most of the 2006-2022 fishing activity tended to occur year-to-year – in other words, geospatial centres of gravity calculated as the catch-weighted average of sessions' fishing grid cell centroid longitude and latitude per year; and (5) sessions' average annual to annual monthly duration/CPUE/ location water depth. The Pearson correlation coefficient was employed as a measure of relevant variables' linear association (Zou et al. 2003); and averages were calculated as the unweighted or weighted arithmetic mean as applicable, after grouping data by the appropriate variable/s (e.g., year-month).
- Chapter 4 reports on (1) formulation and mean estimated hold-out CV:RSMPE-based performance of the 4 GAMs ultimately assessed as candidates for describing relevant spatial-temporal diel-type variations in session-level chokka jig CPUE; (2) the best performing candidate's formula specification after ultimately 4 iterations of using the *mgcv*::*k.check* function to evaluate and subsequently increase *k* for relevant smooth terms, to allow for an adequate degree of non-linearity in the to-be-interpreted model's fit to the full modelling data set; and (3) the final selected candidate's refined formulation's validity as a 'useful' model – in other words, what did *tweedie* GAM diagnostics show as to the said model's residual, assumptive and posterior predictive goodness-of-fit. It should be noted that day-of-year was presumed to be an appropriate variable in investigating seasonal trends/patterns.
- Chapter 5 addresses the answering of research questions stated in Section 1.5. Model-based prediction was employed in estimating the response at varying levels/values of predictor variables relevant to answering a research question and a constant

level/value per non-pertinent predictor variable. This enabled investigating differences/variations in CPUE estimates specific to (1) the effect of day vs night; (2) the effect of day vs night per day-of-year of 365 days-of-the-year; (3) the effect of day vs night at each centroid longitude-latitude included in the model (i.e., fishing grid cells where at least a single session-level catch had been recorded in the modelling data); and (4) the 2006-2022 average for the effect of day vs night per day-of-year at each centroid longitude-latitude included in the model (i.e., predictions were for the combined effect of $day/night$ on $day-of-year_{i=1,2,\ldots,n}$ in $year_{i=2006,2007,\ldots,2022}$ at $centroid_{i=1,2,\ldots,n}$, and model estimates' arithmetic means were calculated for day/night per day-of-year per centroid regardless of year). With (4), model estimates were processed to pertain to the average year in order to simplify the interpretation and reporting of spatial-temporal results. The reporting and interpretation of investigative results were done in a mostly qualitative manner, as estimated CPUEs were visualised in order to note and describe spatial and, or temporal trends/patterns in terms' marginal effect/s on the response.

Chapter 3: Results – Data exploration

Filtered-cleaned catch record data were explored following Sections 2.3 and 2.5, to investigate spatial to temporal aspects deemed interesting or pertinent to informing modelling-related procedures during the course of the study. There seemed to be indications of correlation between the number of jigging sessions and total catch made within a year (See Figure 7). However, such correlation needs to be interpreted with caution as it does not equate to causality, since these two variables (and their interrelation) naturally result from complex multidimensionality unaccounted for in Figure 7.

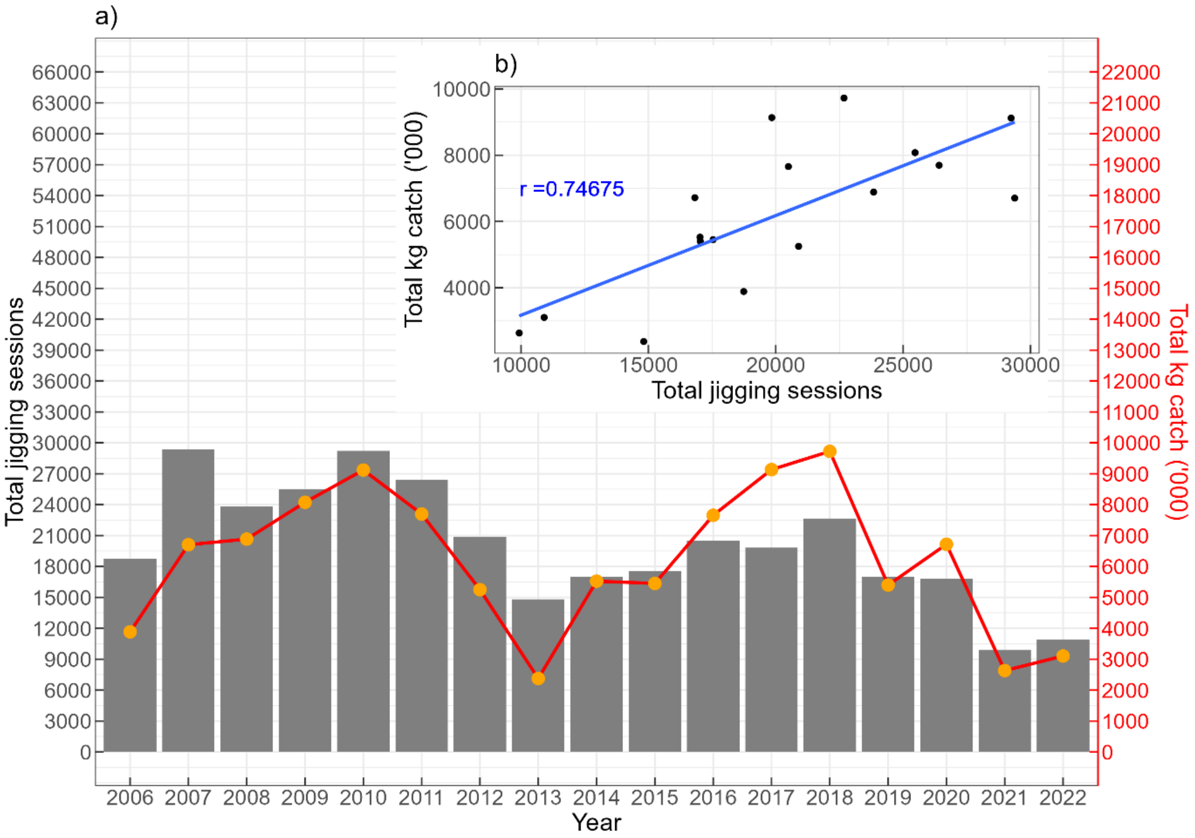


Figure 7: a) Total number of jigging sessions and kg squid jig catch landed per annum (2006-2022), with the barplot graphed according to the lefthand y-axis and line-dot plot according to the righthand y-axis. b) Correlation between annual total number of jigging sessions and total kg squid jig catch landed for 2006-2022, showing the Pearson Correlation Coefficient (r = 0.74675).

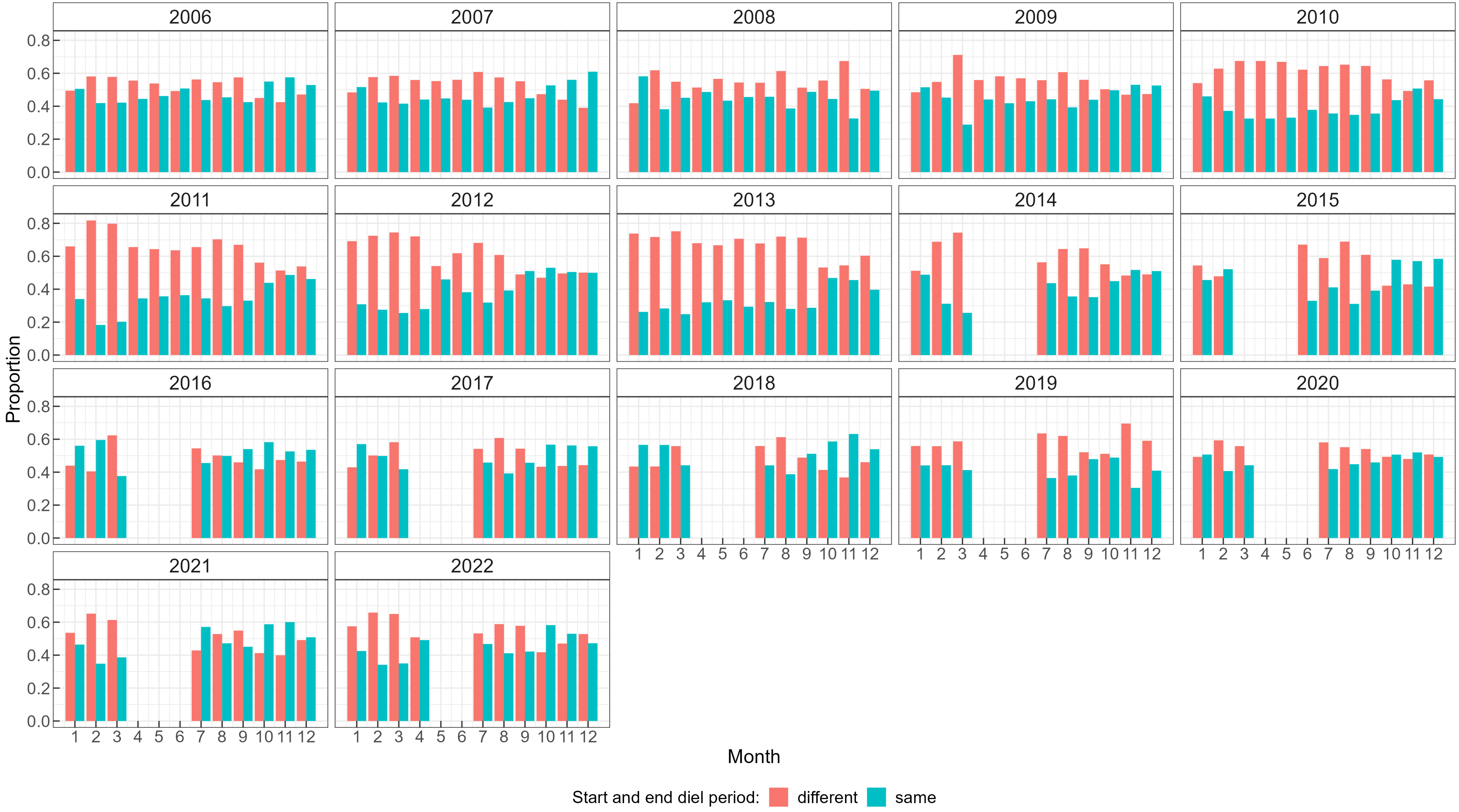


Figure 8: Per month per year proportion of 2006-2022 jigging sessions started and ended in the same or a different diel period.

Figure 9: Per month per year proportion of 2006-2022 jigging sessions carried out at nautical dawn, day, dusk or night when started and ended in the same diel period.

There also seemed to have been a similar proportion of sessions started and ended during the same and different diel time periods since 2014 (See Figure 8). When started and ended during the same time period, most 2006-2022 sessions seemed to have been carried out purely at day or night (See Figure 9). In addition, purely nighttime sessions appeared to have occurred more during winter while purely daytime sessions seemed to have been carried out more during summer (See Figure 9).

The data seemed to furthermore indicate an overall trend of larger catches mostly resulting from relatively shorter jigging sessions in recent years (See Figure 10), following an Eastward shift in the spatial distribution of most fishing activity over time (2006-2022) (See Figure 11). Similarly, a greater magnitude of minutes jigged did not always equate to a larger rate of catch per session, from month to month across years. For example, in July and August, sessions' duration tended to be above average while catch rates were mostly below average, with sessions mostly carried out at above average water depths. Whereas, in December, the reverse was mostly true with a tendency for nominal CPUE to be higher and sessions' duration to be shorter than average, with sessions mostly carried out at depths below annual averages (See Figure 12, Figure 13, Figure 14). However, it should be noted that March 2014 appeared to be a notable outlier with regard to mean jigging session length (See Figure 12), while February 2011 appeared the same with regard to session locations' mean reported water depth (See Figure 14).

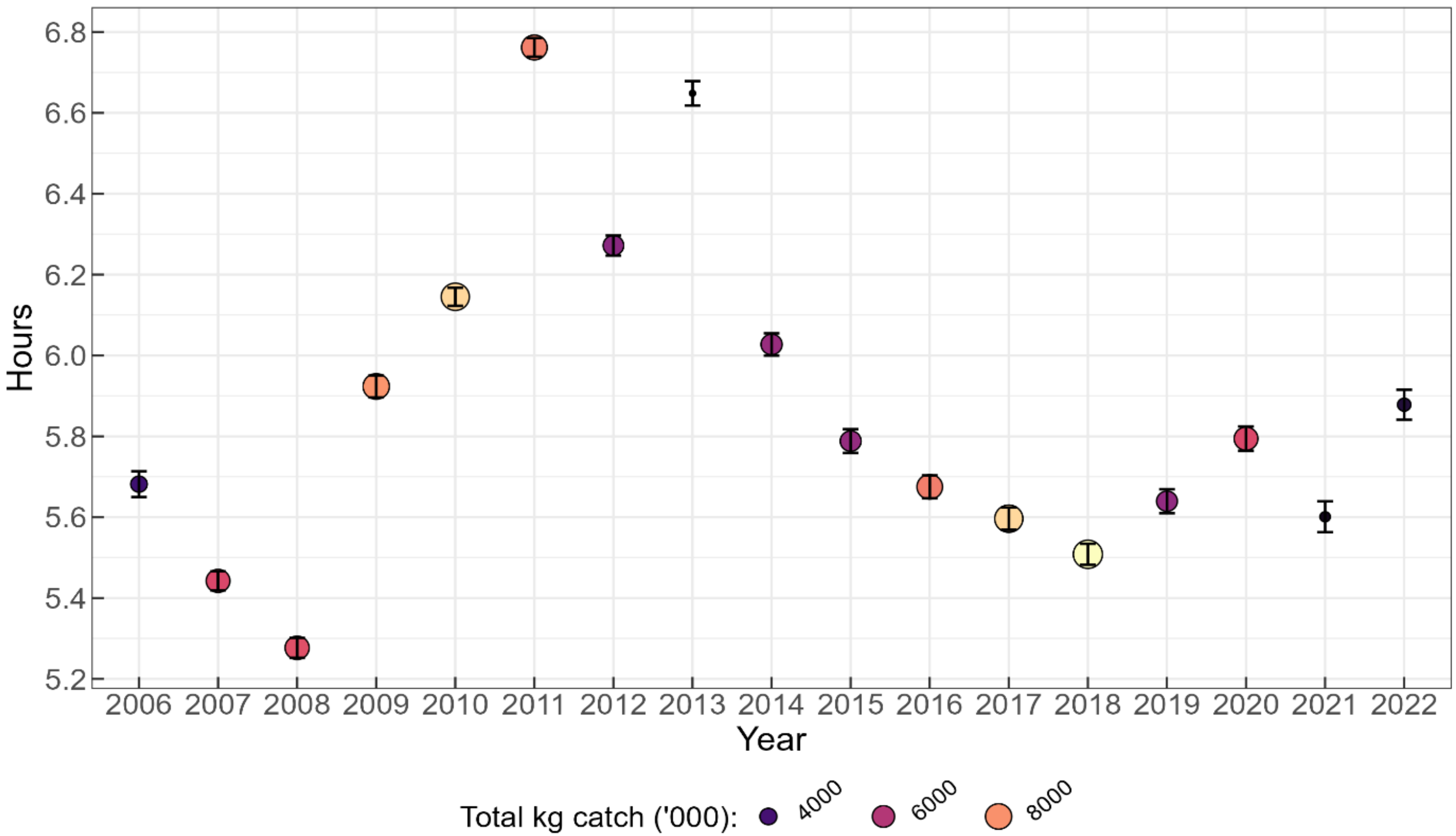


Figure 10: Annual mean and Standard Error of the Mean of 2006-2022 jigging sessions' duration alongside total kg squid jig catch landed per annum.

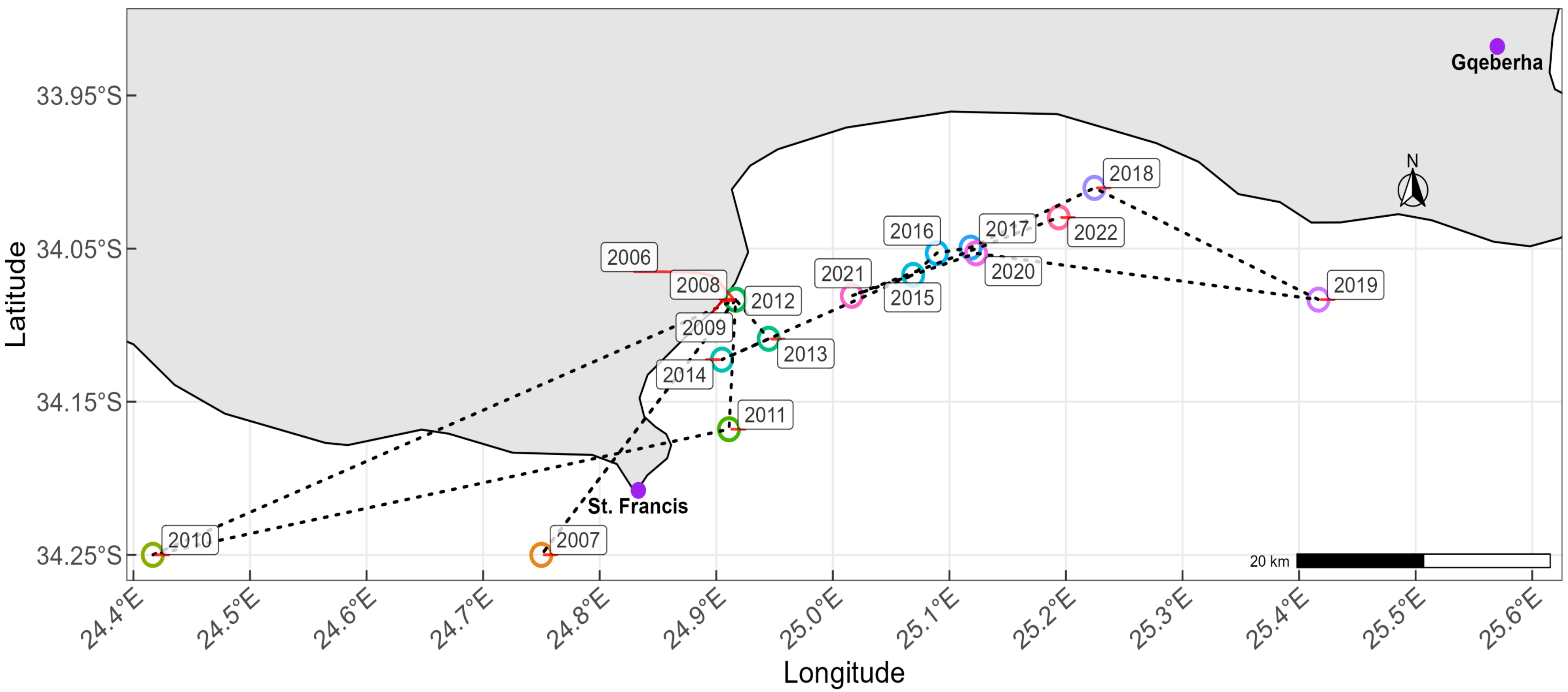


Figure 11: Sessions' geospatial centre of gravity per annum (2006-2022), as weighted by the catch ("kgTotal") landed per session.

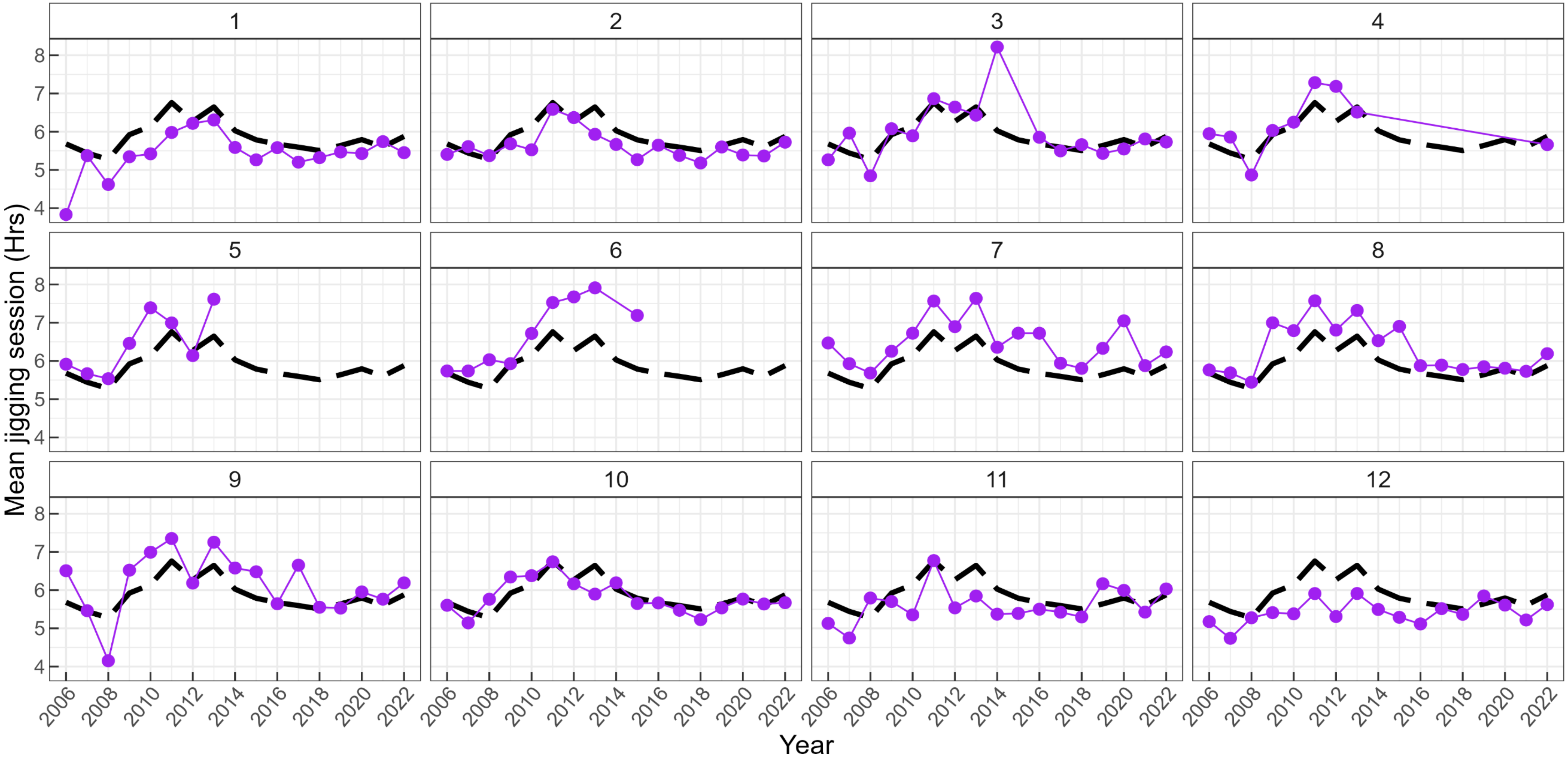


Figure 12: Mean jigging session length. Dashed black lines indicate annual averages across months. Purple line-dots indicate month-specific averages per year. Long-term average: 5Hrs and 51mins.

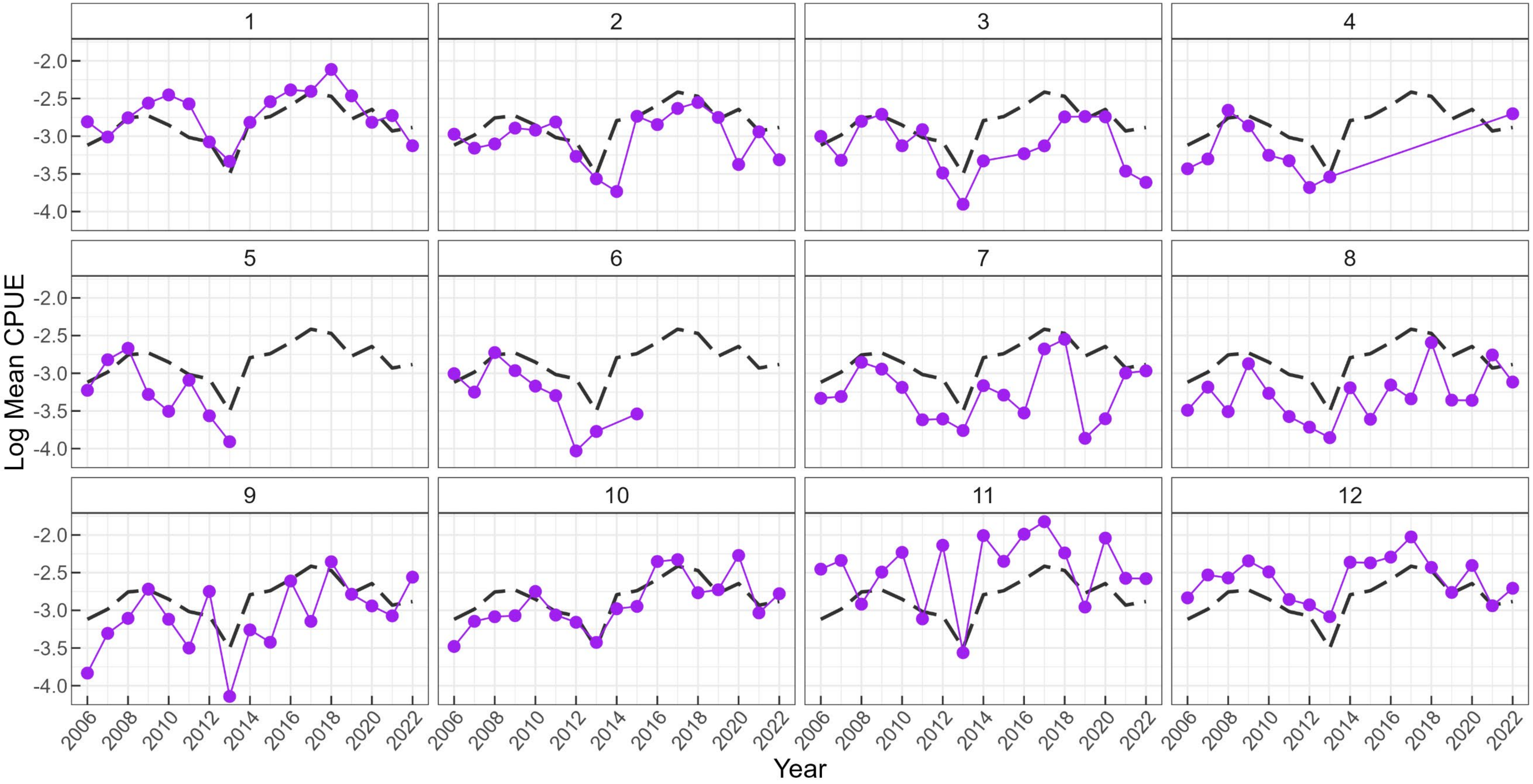


Figure 13: Jigging sessions' mean monthly nominal CPUE by year. Dashed black lines indicate annual averages across months. Purple line-dots indicate month-specific averages per year.

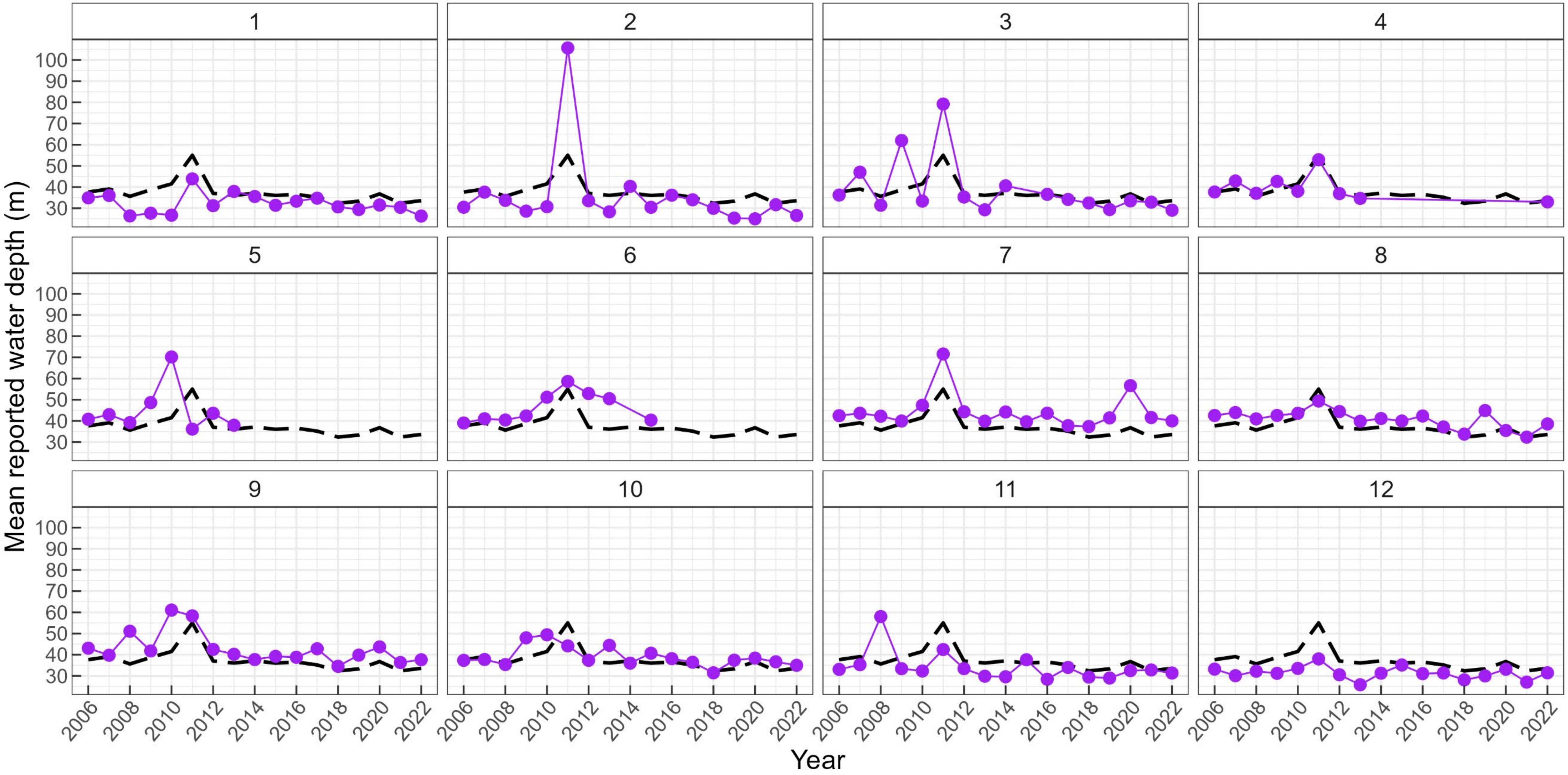


Figure 14: Jigging session locations' mean reported water depth. Dashed black lines indicate annual averages across months. Purple line-dots indicate month-specific averages per year. Long-term average: ~38.07m.

Chapter 4: Results – Model selection and validation

This chapter reports on procedural to analytic outcomes of the study's model selection-refinement-validation stages, following Sections 2.4.2 and 2.5. These stages served to best ensure research questions were ultimately addressed through the employ of a best-performing model, optimally refined in its goodness-of-fit.

4.1 Selection

Table 1: Candidate model formulas. "during" specified night or day, "DOY" specified the day-of-year, "block_midLon" and "block_midLat" respectively specified relevant Fishing grid cells' centroid longitude and latitude, "minutesTotal" specified the total minute duration of a jigging session, "pointBathyMeter" specified session locations' reported water depth in meters, and "factor_vessel" specified the relevant jigging vessel as a factor in model formulation. Grid cell centroid coordinates were used due to pre-2014 data not including sessions' point specific coordinates.

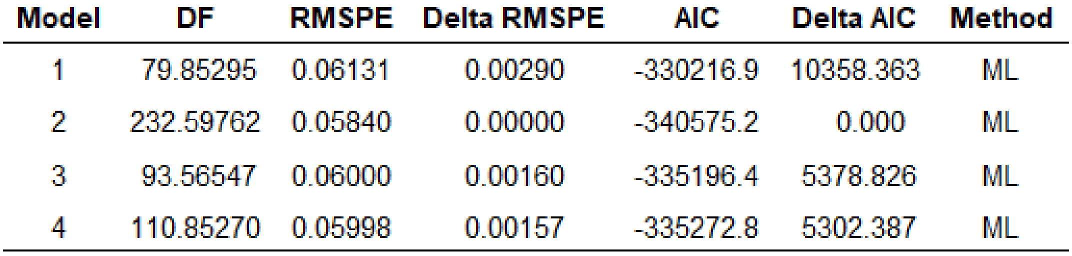
Model	Formula
1	minuteCPUE ~ during + s(DOY, by = during) + s(year, by = during) + s(block_midLon, block_midLat, by = during)
2	minuteCPUE ~ during + s(DOY, by = during) + s(year, by = during) + s(block_midLon, block_midLat, by = during) + s(minutesTotal) + s(factor_vessel, bs = "re")
3	minuteCPUE ~ during + s(DOY, by = during) + s(year, by = during) + s(block_midLon, block_midLat, by = during) + s(minutesTotal) + s(pointBathyMeter)
4	minuteCPUE ~ during + s(DOY, by = during) + s(year, by = during) + s(block_midLon, block_midLat, by = during) + s(minutesTotal) + s(pointBathyMeter) + ti(block_midLon, block_midLat, pointBathyMeter, d = c(2, 1))

Candidate models were formulated as specified in Table 1 and, as shown in Table 2, estimated for comparison according to Maximum Likelihood (ML) instead of Restricted Maximum Likelihood (REML). Model 1 was fully nested in Model 2, 3 and 4, constituting a base of predictors and predictor interactions, deemed necessary to answer study research questions

(See Table 1). However, computational difficulties prohibited full nesting of all earlier models in all later formulations. Hence, Model 2, 3 and 4 involved the added inclusion of carefully considered terms, deemed to be of note in explaining variations in CPUE (See Table 1). With regard to candidate model estimations, the relevant approach was taken due to ML being better suited for the comparison of models differing in 'fixed' effects (Zuur et al. 2009, Wood 2017), all candidate models differing in their 'fixed' effects and only a single model also incorporating a random effect smooth in its formulation (See Table 1).

Model selection resulted in Model 2 being deemed the most optimal choice. This model seemed to have the least predictive error (RMSPE) on average (See Table 2).

Table 2: Candidate model hold-out Cross Validation metrics. "DF" specifies models' estimated degrees of freedom. RMSPE and AIC (Akaike Information Criterion) specify the mean of relevant statistics calculated over 10 iterations. Delta statistics were calculated using related neighbouring columns as relevant. "ML" stands for Maximum Likelihood.



Model	DF	RMSPE	Delta RMSPE	AIC	Delta AIC	Method
1	79.85295	0.06131	0.00290	-330216.9	10358.363	ML
2	232.59762	0.05840	0.00000	-340575.2	0.000	ML
3	93.56547	0.06000	0.00160	-335196.4	5378.826	ML
4	110.85270	0.05998	0.00157	-335272.8	5302.387	ML

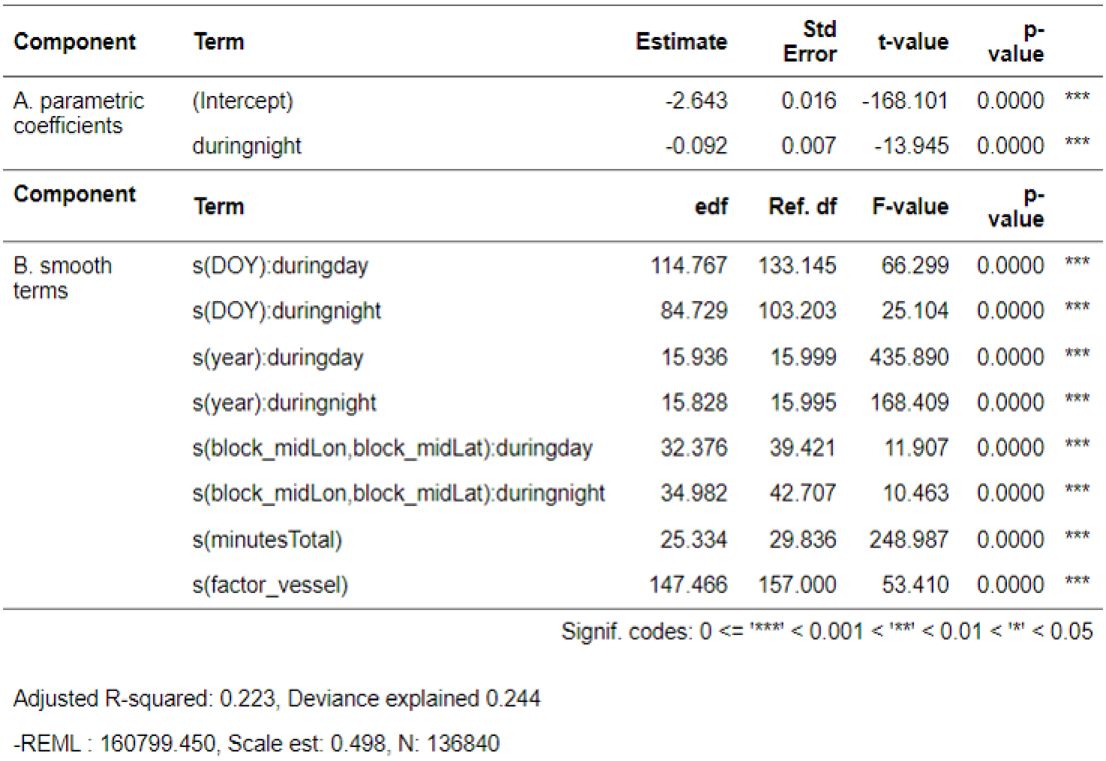
The refined formulation of the final selected model can be specified as

CPUE = during + s(DOY, by = during, k = 160) + s(year, by = during, k = 17) + s(block_midLon, block_midLat, by = during, k = 60) + s(minutesTotal, k = 40) + s(factor_vessel, bs = "re")+ ε

where:

"s" indicates a smoothing spline, "k" the spline basis dimension, 're' a random effect smooth estimated by the *mgcv* modelling engine, and ε the random error (Wood 2003, Wood 2011, Wood et al. 2016, Wood 2017). The model was fitted by Restricted Maximum Likelihood and all included terms were estimated to be statistically significant in their effect on the response (See Table 3).

Table 3: The final selected model's summary.



Component	Term	Estimate	Std Error	t-value	p-value	
A. parametric coefficients	(Intercept)	-2.643	0.016	-168.101	0.0000	***
	duringnight	-0.092	0.007	-13.945	0.0000	***

Component	Term	edf	Ref. df	F-value	p-value	
B. smooth terms	s(DOY):duringday	114.767	133.145	66.299	0.0000	***
	s(DOY):duringnight	84.729	103.203	25.104	0.0000	***
	s(year):duringday	15.936	15.999	435.890	0.0000	***
	s(year):duringnight	15.828	15.995	168.409	0.0000	***
	s(block_midLon,block_midLat):duringday	32.376	39.421	11.907	0.0000	***
	s(block_midLon,block_midLat):duringnight	34.982	42.707	10.463	0.0000	***
	s(minutesTotal)	25.334	29.836	248.987	0.0000	***
	s(factor_vessel)	147.466	157.000	53.410	0.0000	***

Signif. codes: 0 <= '***' < 0.001 < '**' < 0.01 < '*' < 0.05

Adjusted R-squared: 0.223, Deviance explained 0.244

-REML : 160799.450, Scale est: 0.498, N: 136840

4.2 Validation

Residual diagnostic plots seemed to indicate a sub-optimal fit to the data (See Figure 15). A quantile-quantile plot showed slight deviation from what is expected under the assumed *tweedie* probability distribution, especially in the tail-ends of residuals, although the model was shown to conform to a theoretical *tweedie* distribution of the form $1 < p < 2$ with p estimated as 1.99 (See Figure 15.a). However, standard deviation was mostly within the margin of 1 residual from zero as indicated by Residual vs Linear predictor (See Figure 15.d), Residual density distribution (See Figure 15.b), and Residual vs Session duration and Residual vs Session reported water depth plots (See Figure A1, Figure A2). Also, with deviance residuals as a proxy, error terms seemed to have an approximately normal distribution (See Figure 15.b); and deviance residuals were deemed to be adequately homoscedastic (See Figure 15.d, Figure A1, Figure A2).

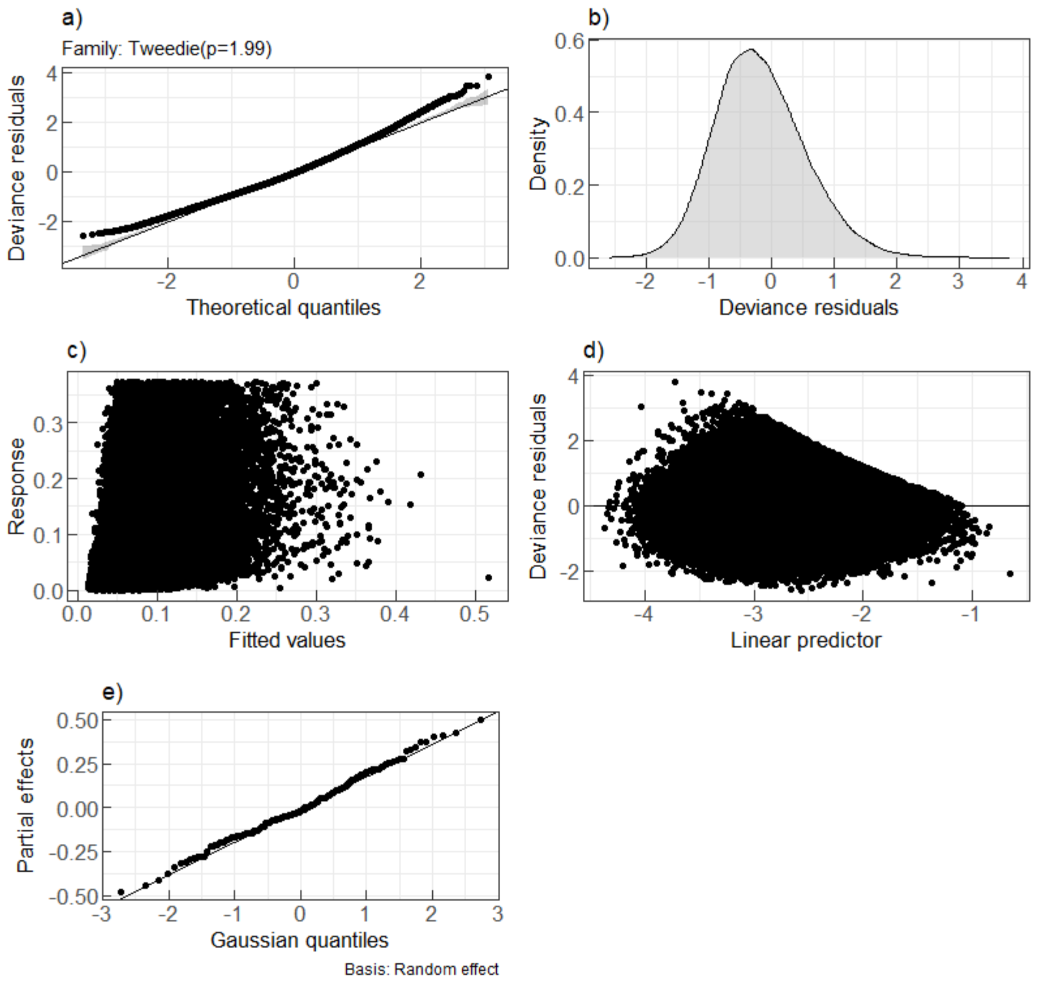


Figure 15: Residual diagnostic plots – a) Overall model quantile-quantile conformity to a *tweedie* distribution; b) Residual probability distribution; c) Observed (Response) vs Model fitted values; d) Residuals vs Fitted values (on the Linear Predictor scale); e) Quantile-quantile conformity of the random effect smooth s(factor_vessel, bs = 're') to a Gaussian distribution.

Visual assessment of spatial pattern in the residuals appeared to indicate a random distribution without regions of low and high residuals (See Figure B1, Figure B2). And relevant outputs from *DHARMa* (Hartig 2022) showed neither spatial- nor temporal-autocorrelation were statistically significant (i.e., p≥0.05; Moran's I test for distance-based autocorrelation: observed = -0.011184, expected = -0.005102, sd = 0.008358, p-value = 0.4668; Durbin-Watson test: DW = 2.355, p-value = 0.4517).

Concurvity seemed to be fairly low for most model terms. However, overall estimated concurvity was shown to equal one for parametric terms. Smooth-wise partitioning showed such perfect concurvity to occur between model parametric terms (i.e., “during”) and the factor-type random effect smooth of “factor_vessel” (See Figure C1, Figure C2). This was to be expected and deemed non-problematic considering “during” comprised of only 2 factor levels, “day” and “night” (Simpson 2022). In addition, the model’s random effect smooth was shown to approximately conform to a Gaussian distribution (See Figure 15.e).

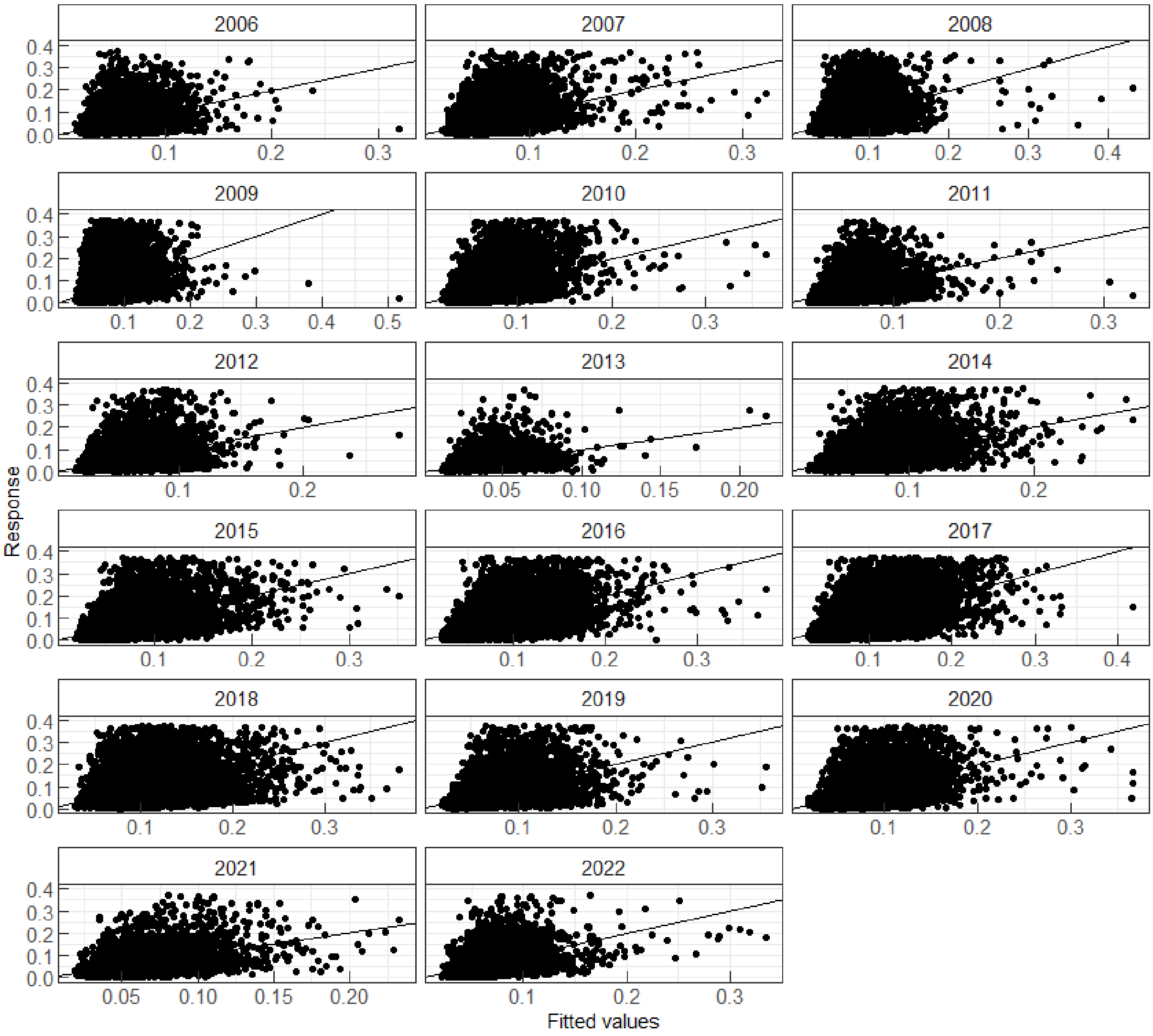


Figure 16: Observed (Response) vs Fitted values plotted by year with a 1:1 ratio line, for visual estimation of correspondence between model predictions and observed values.

Observed (Response) vs Fitted value plots seemed to show adequate correspondence between actual and model predicted CPUE overall (See Figure 15.c) and for most years (See Figure 16). However, there appeared to still be some tendency of fitted values being higher than those observed in the data since Figure 16 also indicated partial (model) overestimation of observed data values in some years. Further, boxplots indicated most residuals were <0 when plotted by month and year per diel period (See Figure D1, Figure D2).

Posterior Predictive Checks seemed to indicate adequate overlap of empirical (blue) and model simulated (grey) CPUE per diel period (See Figure 17). That is why the model was inferred to be fairly accurate in its simulation-recovery of actual day and night catch rates (See Figure 17).

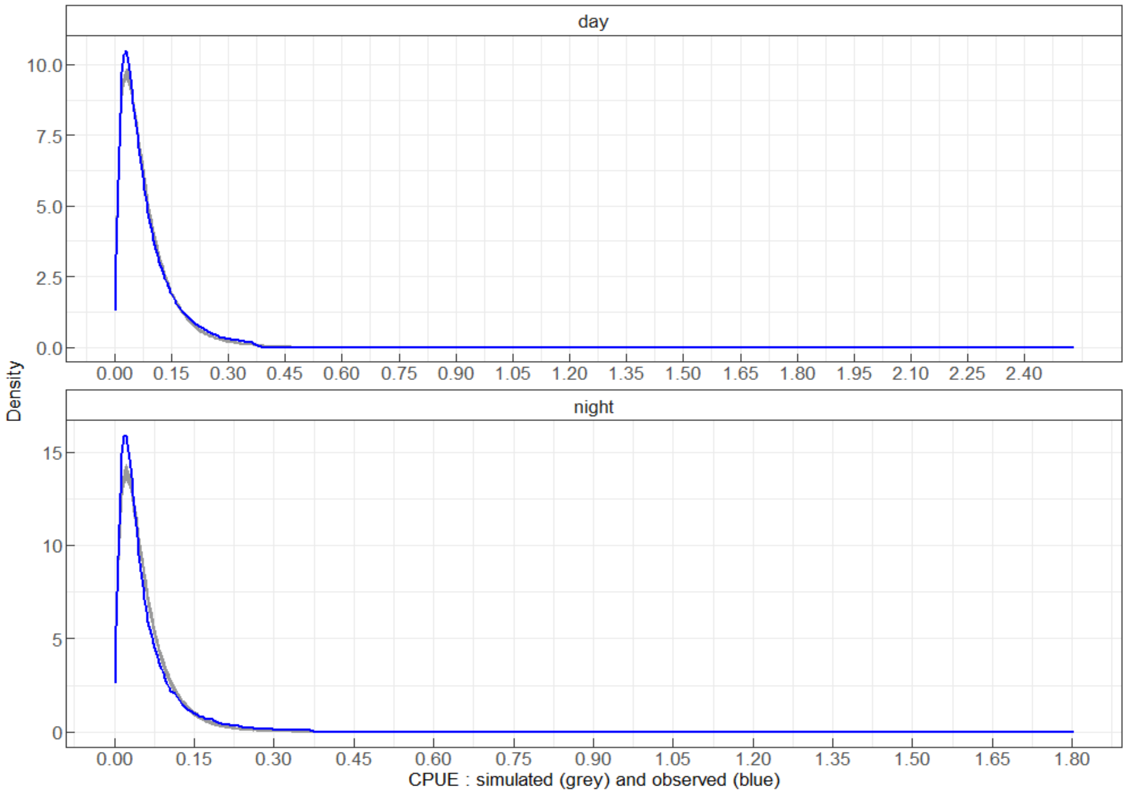
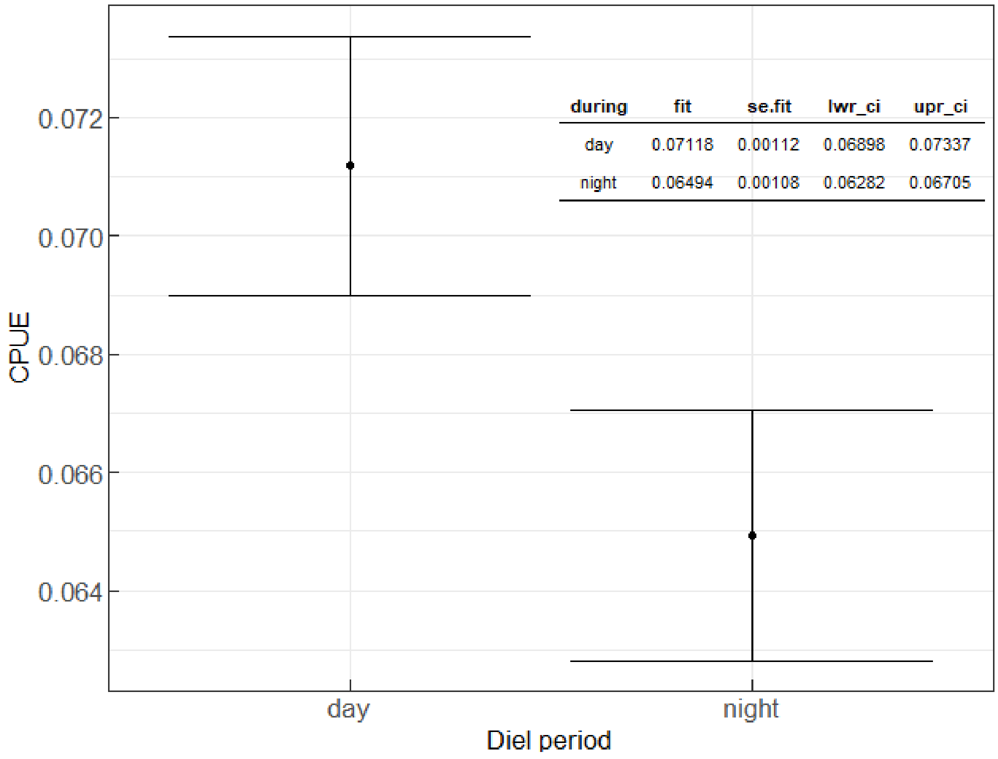


Figure 17: Model Predictive Check with simulation of 200 draws from the posterior distribution.

Chapter 5: Results – Model interpretation

5.1 Is there an effect of diel period on chokka CPUE?

The model indicated chokka catch rates tended to be higher during daytime (See Figure 18). Shown in Table 3; the parametric term for diel period was estimated to be statistically significant in its effect on the response (0 ≤ p-value < 0.001), with mean CPUE estimated to differ from day to night by a value of -0.092 on the predictor scale. However, these results do not indicate and it thus remains uncertain whether such a day vs night difference is statistically significant.



during	fit	se.fit	lwr_ci	upr_ci
day	0.07118	0.00112	0.06898	0.07337
night	0.06494	0.00108	0.06282	0.06705

Figure 18: Model-based estimation for the marginal effect of the parametric terms for diel period. Errorbars indicate 95% confidence intervals. Inserted text shows model estimated point response-scale values (“fit”) and standard errors (“se.fit”), and calculated confidence intervals’ lower (“lwr_ci”) and upper (“upr_ci”) limit per level of the factor for diel period (“during”).

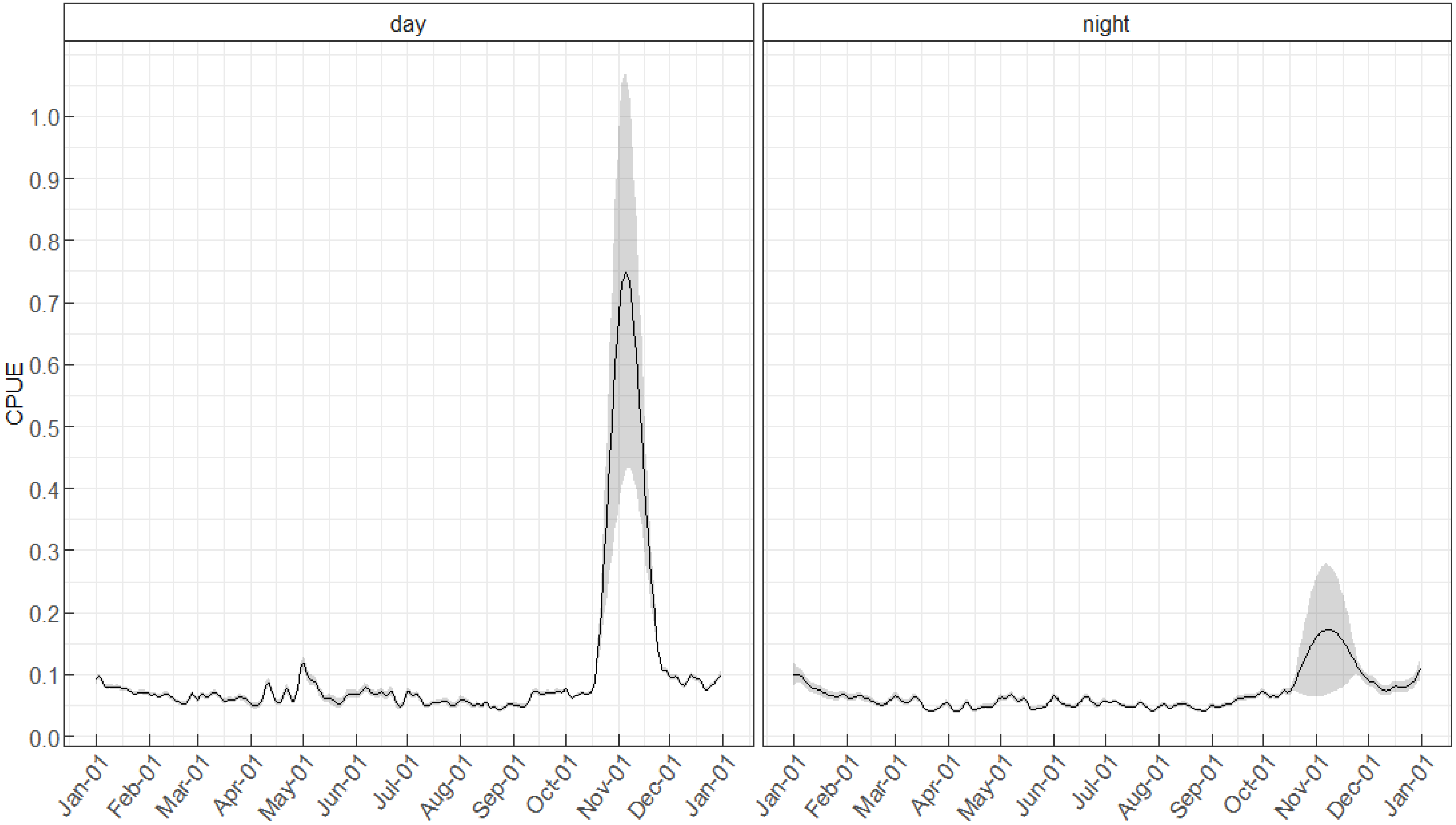


Figure 19: Model-based estimation for the combined marginal effect of day-of-year and diel period. The x-axis shows day-of-year at a monthly interval after converting to date. Confidence bands indicate 95% confidence intervals.

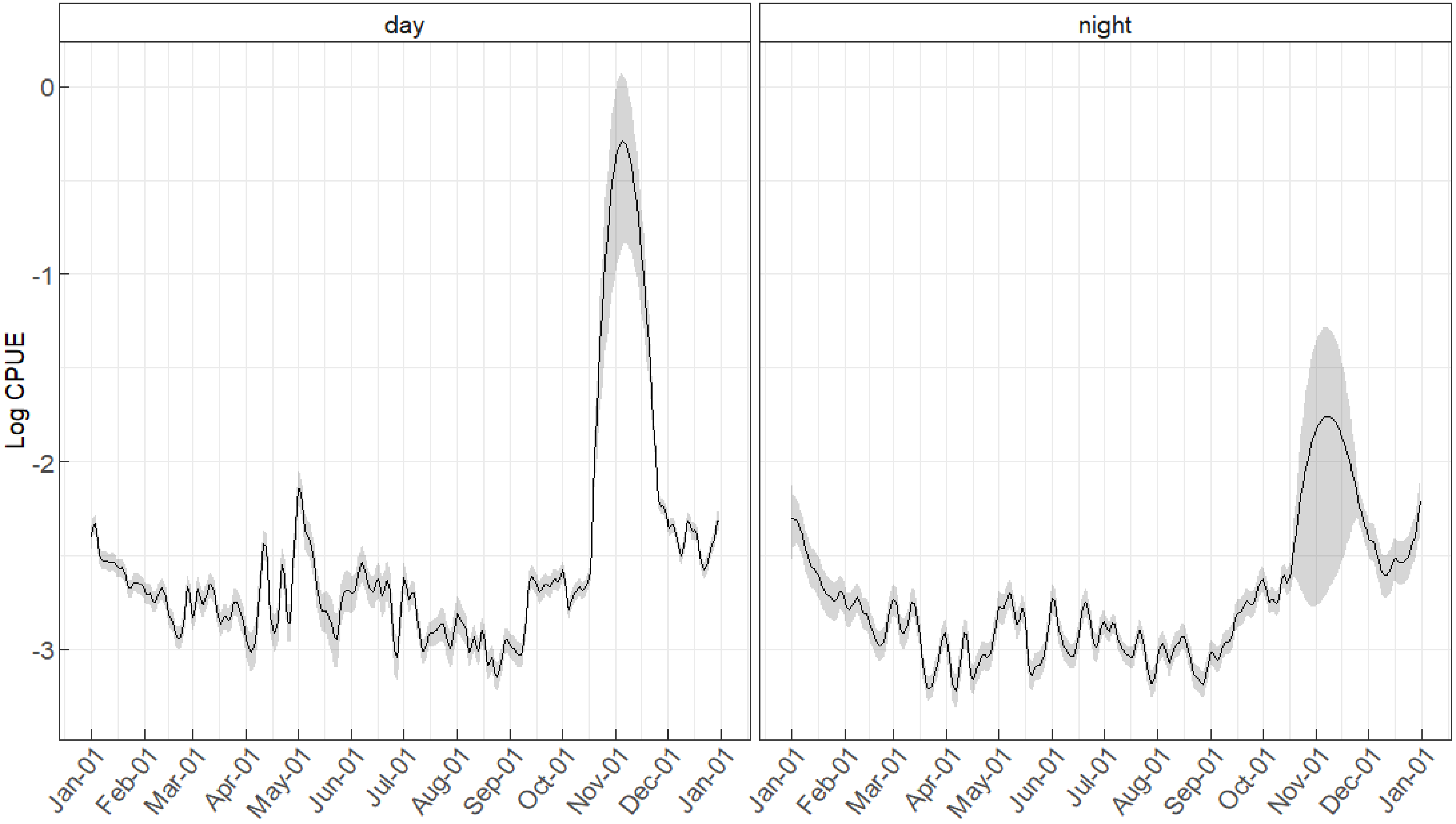


Figure 20: Model-based estimation for the combined marginal effect of day-of-year and diel period, on the log scale. The x-axis shows day-of-year at a monthly interval after converting to date. Confidence bands indicate 95% confidence intervals.

5.2 Is there seasonal variation in any effects of diel period on chokka CPUE?

The model indicated clear season-type day-of-year trends in catch rates with a surge in day-night chokka CPUE from October to January, peaking around October-December, with mostly higher catch rates during daytime. There also seemed to be minor surges in daytime CPUE between April and June, when nighttime catch rates remained relatively low (See Figure 19, Figure 20).

5.3 Is there spatial variation in any effects of diel period on chokka CPUE between seasons and years?

With visual spatial-temporal comparisons of model predicted values, catch rates seemed higher during daytime across most of the modelled fishing grounds for most of the average year (See Multimedia 1). However, there also seemed to be finer grained spatial-temporal variations in CPUE within and between daytime-nighttime periods. Around beginning of January to middle of March and middle to end of July, catch rates seemingly tended to be higher both inshore and offshore during nighttime (than at daytime – albeit mostly by a marginal degree) at 20-21°E, with incidence of slightly higher within-day CPUEs appearing to occur more West than East of 20.5°E and slightly higher within-night CPUEs appearing to occur more East than West of 20.5°E (See Multimedia 1). During these same time periods, at 24-26°E, slightly higher nighttime CPUEs seemed to occur offshore (compared to inshore), with seemingly no clear delineation in higher/lower daytime catch rates. The model also seemed to indicate consistency in higher daytime (than nighttime) CPUE in the inshore-offshore around 22-24°E and offshore at ~33.5-34.5°S – ~27.5-29°E, across the average year. In the inshore-offshore around 22-24°E, daytime (compared to nighttime) CPUEs seemingly tended to be slightly-to-moderately higher for most of the average year and higher to an extreme degree around end October-middle November (See Multimedia 1). In the offshore at ~33.5-34.5°S – ~27.5-29°E, daytime (compared to nighttime) CPUEs seemingly tended to be moderately-to-extremely higher for most of the average year – arguably due, in part, to the lowest within-night CPUEs, across the modelled fishing grounds, appearing to occur mostly in the offshore at ~33.5-34.5°S – ~27.5-29°E (See Multimedia 1). Similar trends and patterns seemed to be indicated with the model’s estimation of spatio-diel marginal effects on CPUE (See Figure 21).

Multimedia 1: Log of mean model predicted day/night chokka CPUE on the South African commercial squid jig fishing grounds, 2006-2022. Animated at 1 frame per second for 366 frames. Click ▶ to play or access as available at: https://zivahub.uct.ac.za/articles/media/Log_of_mean_predicted_Day_Night_Chokka_CPUE_on_the_South_African_commercial_squid_jig_fishing_grounds_2006-2022_/27079114?file=49329688. Averages were calculated after grouping by DOY, diel period and Fishing grid cell.

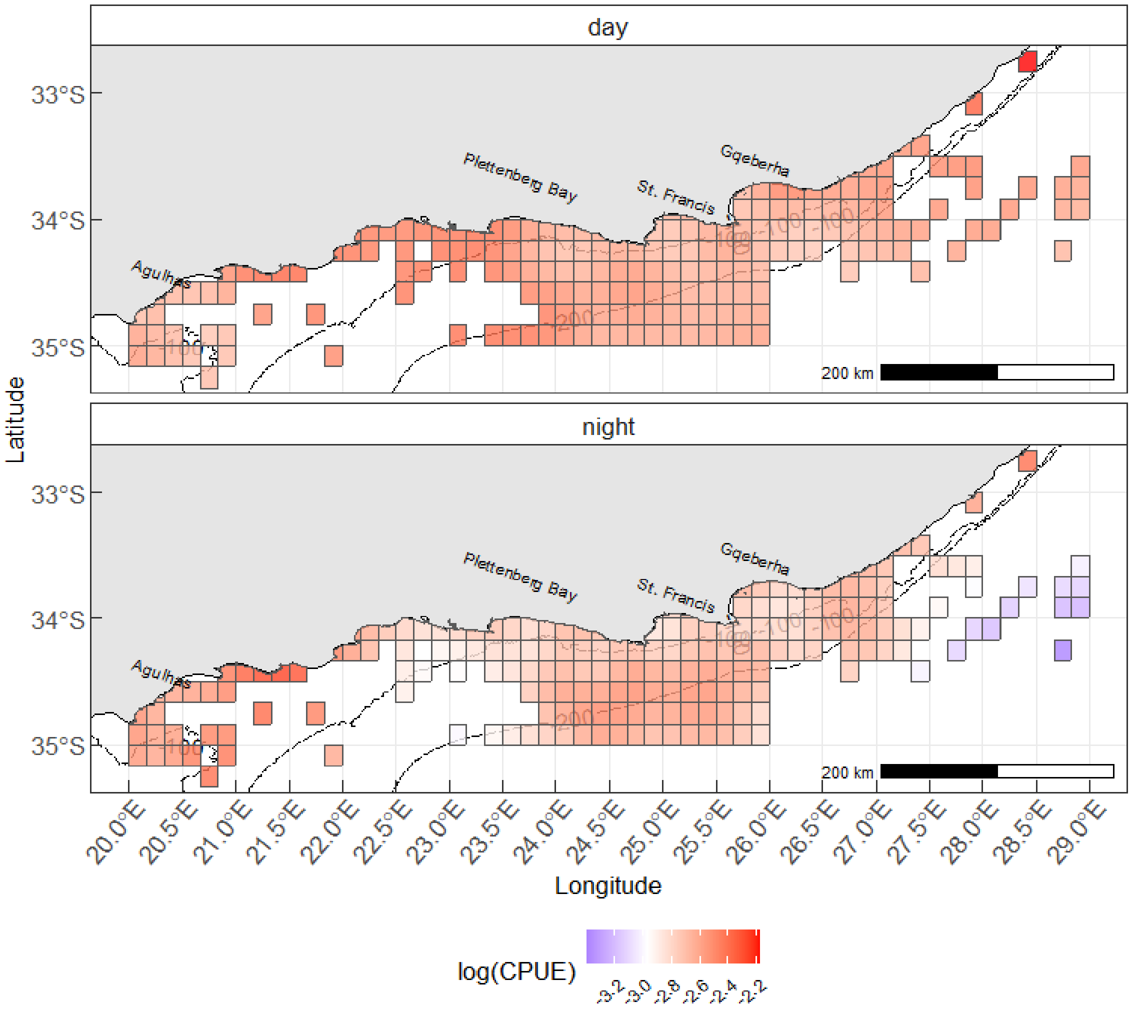


Figure 21: Model-based estimation of spatio-diel marginal effects on chokka CPUE.

Chapter 6: Discussion

This study looked at whether commercial squid jig fishery records reveal any diel, diel-seasonal and spatio-diel to spatio-seasonal patterns in Catch Per Unit Effort (CPUE) of adult *L. reynaudii* (chokka) on the relevant fishing grounds of South Africa. Chokka are a unique and dynamic part of global biodiversity (See Chapter 1) and form the base of South Africa's third most lucrative fishery (DFFE 2023). That is why the Fisheries Management Branch of the South African Department of Forestry, Fisheries and the Environment (DFFE:FB) employs relevant scientific research to inform collaborations between government and industry, in managing the commercial chokka jig fishery towards optimal social-ecological sustainability (See Chapter 1). As part of this, recent deliberations have led to calls for using relevant catch records to assess diel-type variations in commercial jig fishing and aggregate chokka behaviour throughout the year (See Chapter 1). Hence, this study was one of the first to employ DFFE session-level commercial squid jig logbook catch records in taking a model-based approach, to investigate:

1. Is there an effect of diel period on chokka CPUE on the commercial squid jig fishing grounds of South Africa?
2. Is there seasonal variation in any effects of diel period on chokka CPUE on the commercial squid jig fishing grounds of South Africa?
3. Is there spatial variation in any effects of diel period on chokka CPUE between seasons and years on the commercial squid jig fishing grounds of South Africa?

Project modelling procedures led to selection, validation and interpretation of a final model (Model 2; See Table 1, Table 2) describing 24.4 % of the deviance (See Table 3) (Wood 2017). Any model-based trends and patterns needed to be interpreted with caution, especially when estimated for April-June and October-November periods. *Inter alia*, previously published model-based considerations (of commercial chokka jig CPUE) include studies arguably more robust in terms of empirical science. For example, unlike the present study's use of fisheries-dependent session-level third-party data, Schön et al. (2002)[10] seemed to employ more stringent, fisheries-independent sampling on a minute-to-minute – hour-to-hour basis, *in situ* of commercial jigging operations (Schön 2000, Schön et al. 2002). In addition, the present study's April-June model results were mostly informed by 'old' pre-2014 data, records prior to the practice of a closed jigging season during autumn-winter each year; and October-November model results involved an arguably notable degree of interpolation, due to the annual practice of a closed jigging season in late spring – 19 October-23 November – since 1993 (See Chapter 1). However, it remains true that this study pertained to chokka-dedicated commercial data reported by 158 vessels over a total period of 4,609 'fishing days' ($\bar{x}$: ~665.14 ± ~30.85 (Standard Error of the Mean) 'fishing days' per 'fishing' vessel). In addition, the study's selected Model 2 enabled partially controlling for the 'human' factor when investigating relevant terms' marginal effects, via its account of operation-type influences on CPUE (i.e., vessel-type ("factor_vessel") and effort-type ("minutesTotal") effects; See Table 1, Table 2) (Schön 2000, Schön et al. 2002, Hoyle et al. 2024). Hence, it was argued for the present study to be adequately useful in investigating presence of relevant predictors' effect on chokka behaviour.

6.1 Is there an effect of diel period on chokka CPUE?

Results from this study support narratives of a night to day increase in chokka concentrations on the commercial squid jig fishing grounds of the South African southeast coast (See Figure 18). Downey et al. (2010) seemed to posit any high-density aggregative spawning typically occurs at daytime; with squids largely dispersing to rest, migrate to other spawning sites and, or feed after dusk – before dawn. In addressing the effects of such types of patterns on commercial chokka jig catch rates, Schön et al. (2002) seemed to argue within-day/night – between-day/night variations involve differences in the areal prevalence of nighttime feeders

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[10] "...Collection of real-time CPUE and environmental data was carried out by the first author. Eighteen sampling trips, averaging 8.6 days per trip, were conducted on five commercial chokka squid jigging vessels between May 1996 and May 1998, and ranged throughout the main spawning area between Plettenberg Bay and Port Alfred...Factors such as weather, equipment breakdown and irregular sailing dates limited the frequency and duration of trips and resulted in 130.5 effective sampling days..." (Schön et al. 2002; p. 784).

– daytime spawners (i.e., how widespread and dense or dispersed squids are wherever chokka boats choose to jig). Notably: Downey et al. (2010) pertained to 2003-2006 data collected within Kromme Bay of the Cape St Francis – Gqeberha region, part of the arguable core of commercial chokka jig fishing activity, during annual October-November 'seasons' closed to jigging (See Chapter 1); and Schön et al. (2002) involved 1996-1998 catch data collected in <100m deep waters between Plettenberg Bay and Port Alfred (~23° to ~26°E). The present study therefore seemed more generally applicable considering estimations were informed by 2006-2022 data recorded throughout the year, over a wider longitudinal range (20-29°E) and up to greater depths (≤238 m). Hence, a finding of higher daytime catch rates (See Figure 18) seemed to strengthen notions of chokka availability being greater at day than night (i.e., that most spawners often disperse at night to feed; Sauer and Lipiński 1991), since such a pattern presumably enables greater daytime efficiency in the use of handline jigging to commercially target chokka squid.

Any optimal realisation of relatively high CPUEs partly depends on relevant individuals' experience and knowledge of intra-diel variations in 'fish' behaviour (Schön et al. 2002, Mercer et al. 2023). Demersal-bottom trawlers seem to target Loliginid longfin squid (*D. pealeii*) mostly during daylight hours in the northwest Atlantic, Georges Bank – Cape Hatteras region off North Carolina of the United States of America (USA). This is presumably due to maturing *D. pealeii* having a tendency to frequent upper water layers at nighttime and occupy bottom waters during diurnal time periods – leading to higher daytime (bottom) trawl catches (Brodziak and Hendrickson 1999, Hendrickson 2011, Jacobson et al. 2015). On the other hand, in the Victoria – Bass Strait region off southeastern Australia, it seems routine for relevant inshore machine jigging operations to happen at night as maturing Ommastrephid Gould's squids (*Nototodarus gouldi*) feed nocturnally in upper water layers – leading to greater nighttime jigging CPUEs (O'Sullivan and Cullen 1983, Nowara and Walker 1998, Green 2011). These two examples seem to already affirm notions of a linkage between species abundance and relevant practitioners' experiential knowledge in the realisation of large catches and high catch rates. However, it is arguably imperative to ensure consideration of cases more similar to commercial chokka jig fishing in South Africa, where operations involve or rely on aggregations of sexually mature – spawning individuals (See Chapter 1).

The opalescent inshore squid (*Doryteuthis opalescens*) and European squid (*L. vulgaris*) form part of squid species targeted when at a stage of aggregating to spawn on the inshore of some sovereign state territories in their distributional range (Cabanellas-Reboredo et al. 2012a, Zeidberg 2013). In <100 m deep waters off California on the North American West Coast, *D. opalescens* squids seem to be natural demersal daytime spawners and known to nocturnally form potentially large pelagic aggregations. This has led to local commercial harvesting largely involving the use of relatively small vessels with ~30 kw of artificial onboard lighting. These 'light boats' attract and concentrate nighttime aggregations at the water surface for seine-net vessels to harvest with relative ease (Vojkovich 1998, Forsythe et al. 2004, Zeidberg et al. 2006, Zeidberg 2013).

In the case of *L. vulgaris*, harvesting seems to include targeting by recreational inshore jigging vessels in Palma Bay off southwest Mallorca Island (Spain), in the northwestern Mediterranean. Such vessels, prohibited from using artificial lighting to attract squids during hours of darkness, seem to target squids mostly around sunset at ~20 to ~35 m depths. Presumably, squids are then still relatively concentrated on the inshore, when switching from a mode of aggregate-daytime-inshore-spawning to more solitary inshore-offshore nighttime feeding. This seemingly leads to CPUEs being relatively higher with the occurrence of sunset at dusk, when squids have largely started to 'switch gears' and remaining solar irradiance entails sufficient underwater visibility for squids to effectively hunt when encountering jigs (Cabanellas-Reboredo et al. 2012a, Cabanellas-Reboredo et al. 2012b). Combined with findings from this study, these four aforementioned examples arguably confirm that squid CPUE varies according to diurnal and nocturnal behaviours and resultant overall abundance patterns of the ontogenetic stage at which a species is typically targeted for capture, barring marked ignorance of relevant faunal habits. However, there seems to simultaneously be a need for caution in interpreting day vs night chokka CPUE 'abundance' in absolute terms, also based on these examples.

Aforementioned examples seem to further allude to higher chokka CPUEs also hinging on relatively abundant squids being in adequate proximity to commercial vessels, and fishers' ability to repeatedly deploy and retrieve gear in a timely manner. *Inter alia*, this relates to interplays between the size of a spawning aggregation and number of vessels attempting to harvest from said aggregation – the smaller an area of active spawning, the smaller the number of vessels able to anchor directly over said aggregation and thus have the best catch rates (Sauer 1995). Meaning CPUEs will remain relatively low if squids are abundant in an area and fishers know squids to be abundant within that area, but conditions and, or circumstances do not allow jiggers to catch at a fast rate. For example, Schön (2000) seemed to observe a tendency for chokka boats to move further offshore and use artificial lighting at nighttime, to attract squid dispersed in 50-70m deep waters. Based on this, Schön (2000) seemed to argue that a daytime to nighttime decrease in CPUE is then expected considering nighttime dispersal entails a lower squid-jig encounter rate, even with the use of lights, and that handline jigging becomes more cumbersome in deeper (offshore) waters. However, in terms of the modelling context of this study, such variable influences on session-level chokka jig CPUE are indeterminable.

Model selection procedures did not result in final parameters' consideration of day-night differences in reported water depth with this study. However, *a posteriori* exploration of the raw modelling data seemed to indicate the main grounds for commercial jigging and squid aggregates were located on the relative inshore (i.e., waters <50 m deep; See Figure E1.a), mostly exploited in daytime spring-autumn (See Figure E1.b)[11]; and that there was a tendency for jiggers to exploit deeper-water squid stocks (i.e., waters ≥50 m deep) more during autumn-spring than spring-autumn[12]. Also, jigging operations were presumed to entail utilisation of the same (e.g., 'offshore') squid stocks as demersal trawlers, vessels which occasionally take adult squid as bycatch, when conducted in areas not closed to commercial trawling (Roel 1998, Currie et al. 2023, DFFE 2023)[13]. Following these *a posteriori* exploratory findings and related deliberations, present model-based findings would arguably be more robust had there been a definite account of bathymetry-related effects on session-level

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[11] It seemed: (1) there was relatively minor incidence to near absence of jig catches in waters ≥50 m deep (See Figure E1.a); and (2) the majority of sessions in <50 m deep waters were carried out at daytime during Sept-Mar (i.e., early spring-early autumn) (See Figure E1.b).

[12] It seemed: (1) there was presence of a gradual nighttime (Apr-Jul) and larger-gradual daytime (Apr-Oct) peak in jigging sessions' frequency in 50-70 m deep waters (See Figure E1.b); and (2) >70 m deep waters were mainly jigged at night, during Feb-Sept (See Figure E1.b).

[13] Trawling frequency in these different depth categories on the South African commercial chokka jig fishing grounds seemingly still needed reporting.

chokka jig CPUE. Hence, it seems advisable for future-related modelling endeavours to also incorporate jigging sessions' location bathymetry in their base of predictors and predictor interactions (See Chapter 4).

6.2 Is there seasonal variation in any effects of diel period on chokka CPUE?

Study results support notions of an overall single Oct-Dec peak and variable spawning throughout the rest of a year on the Central and Eastern Agulhas Bank (See Figure 19, Figure 20). The generally accepted scientific narrative seems to be that sexually mature chokka squids are present on the South African South-southeast coast throughout the year, reproducing inshore and, or offshore as and when oceanographic conditions are appropriately conducive and favourable (See Chapter 1; Augustyn 1989, Sauer et al. 1992, Roberts and Sauer 1994, Sauer 1995, Sauer et al. 1997, Oosthuizen et al. 2002, Schön et al. 2002, Olyott et al. 2006, Olyott et al. 2007, Roberts et al. 2012, Lipiński et al. 2016, Lipiński et al. 2020). However, it also made sense for spawners to potentially differ at finer spatial – temporal scales, for example, in terms of cohorts' life history traits and, or the magnitude of individuals' presence (See Chapter 1).

Following Olyott et al. (2006) and Olyott et al. (2007), cohort-level differences may involve a greater portion of the spawner stock comprising of smaller-younger squids in winter-spring (compared to summer-autumn) – in areas closer to the eastern edge of the Agulhas Bank (compared to areas further west). *Inter alia*, this arguably relates to individuals' ecology 'growing up' – presumably, factors such as food availability, the density of conspecifics within and between schools (greater density leading to stronger competition for resources – less space for individual growth), and the favourability of physical conditions would affect whether pre-adults succeed in sexually maturing earlier while/by undergoing a relatively slow rate of somatic growth (See Chapter 1). However, investigating such detailed life history trends/patterns was outside the purview of the present study.

With regard to within-year variation in adults' year-round presence on the South African South-southeast coast, ecological trends are thought to typically involve patterns of a major 'summer' and minor 'winter' influx of spawning-stage individuals, between August-February (‘summer’) and May-July (‘winter’)[14]. Such patterns are presumed to potentially vary interannually in their exact timing and duration. However, despite the potential for such interannual variations, consensus seems to be that overall adult chokka abundance consistently experiences an annual October-December maximum on the inshore, especially at daytime (Augustyn 1989, Sauer et al. 1992, Olyott et al. 2006, Lipiński et al. 2020, Durholtz and Glazer 2022). This study then seems to largely confirm what has been ‘known’ so far. Relevant results allude, *inter alia*, to an overall annual surge in chokka CPUE ‘abundance’ during October-January, peaking around October-December and especially at daytime (See Figure 19, Figure 20, Figure E2). Meaning it appears there has been no major change in recent years, with regard to spawning-stage chokka mainly aggregating at daytime during spring-summer. However, there seems to still be a need for caution in interpreting presence of such a largely unimodal pattern in annual aggregate ‘abundance’ as interannually continuous in future.

In the Southern California Bight, *D. opalescens* seemingly tend to spawn intensely in bulk over a relatively short period of time when there is predominance of appropriately favourable/conducive oceanographic conditions. Conversely, when prevailing seasonal oceanography is sub-optimal, *D. opalescens* seemingly spawn at a lower intensity, in smaller groups over a longer period of time (Van Noord 2020). Also, in eastern Atlantic-Mediterranean waters, the dynamics of different *L. vulgaris* populations appear to vary geographically, *inter alia* with regard to tendent unimodal or multimodal peaks in spawning activity and the within-year duration of spawning incidence, partly according to differences in the regime and, or cycles of oceanic temperature and productivity (Moreno et al. 2002).

Following the examples above, South African *L. reynaudii* subpopulations cannot be concluded incapable of major multimodal peaks in annual spawning in case of persistent prevalence of appropriately favourable/conducive oceanography in future years (Jury 2020).

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[14] Multimodal loliginid spawning patterns have similarly been described for *D. pealeii* in waters of the Georges Bank – Cape Hatteras region in the northwest Atlantic (Macy and Brodziak 2001); and *L. vulgaris*, *Alloteuthis subulata* and *Alloteuthis media* along the Galician coast in the northeast Atlantic, off northwest Spain (García-Mayoral et al. 2024).

Rather, there seemed to be true albeit indeterminate potential for such multimodal peaks to occur, considering: (1) the interannual uncertainty and biological plasticity inherent to the population dynamics of a weed species such as chokka (See Chapter 1) and (2) that South African chokka subpopulations are known to intra-annually comprise of multiple hatchling/spawner cohorts (Lipiński et al. 2020). For the purposes of this study, however, of arguably greater interest would be nocturnal-diurnal divergence in the seasonality of chokka behaviour (See Chapter 1).

Nighttime(Daytime) chokka boat jigging operations seemed to arguably involve weaker (stronger) bias in impacting spawner sex-size classes. Considering earlier mentioned notions of an October-December – especially daytime – maximum in overall annual adult chokka abundance on the inshore (Sauer et al. 1992, Olyott et al. 2006, Durholtz and Glazer 2022), it was not a complete surprise for present results to indicate an October-December daytime peak in annual CPUE 'abundance' to be accompanied by a lesser nighttime peak (See Figure 19, Figure 20, Figure E2) (Sauer et al. 1992, Olyott et al. 2006, Durholtz and Glazer 2022). However, despite these similarly-timed (greater/lesser) season-type (day/night) peaks in CPUE ‘abundance’, important to keep in mind here is that:

1. South African commercial chokka jigging operations are primarily oriented towards targeting inshore aggregations of actively spawning squid (Sauer 1995, Augustyn and Roel 1998, Roel 1998);
2. active chokka spawning aggregations[15] are seemingly characterised by male-skewed sex ratios causing females’ preoccupation with mating large male ‘winners’ and, or small male sneakers in-between egg depositions, smaller-than-average (sneaker) males employing fast-paced dart-in – dart-out tactics in seeking reproductive

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[15] It seemed to remain unclear whether the formation of aggregative male-female chokka spawning activity requires egg depositions to already be present at a ‘mark’ (e.g., first seeded by lone females after having mated offshore); or whether, around dawn, large males may circle and coalesce into a lek-like aggregation in the vicinity of a historic ‘mark’, drawing in females and other males and thus initiating male-female spawning, as long as upwelling-related conditions are appropriately conducive (i.e., even in the absence of eggs) (Sauer et al. 1992, Sauer et al. 1997, Hanlon et al. 2002, Zeidberg et al. 2004, Downey et al. 2010).

opportunity with already paired-mated females, and large (loner/consort) males contesting each other through agonistic displays and, or interactions for reproductive opportunity with un/paired females (Sauer et al. 1992, Hanlon et al. 1994, Sauer et al. 1997, Hanlon et al. 2002, Olyott et al. 2006); and

3. there appears to be limited incidence of such aggregative male-female spawning activity at night (Sauer et al. 1992, Sauer et al. 1997, Melo and Sauer 2007, Downey et al. 2010).

These factors may arguably lead to (1) all aggregate male-female spawners focussing efforts towards maximising reproductive success, making them less cognisant of – cautious towards external risks such as jigging action (Sauer 1995, Hanlon et al. 2002); and (2) greater chance of more females and, or smaller-sized males being caught with nighttime harvests since aggression/aggression-type behaviours form part of loner/consort males' reproductive ecology, making them more reactive towards jigging action (compared to other sex-size classes) with active spawning mostly during the day (Augustyn 1989, Sauer et al. 1992, Lipiński 1994, Melo and Sauer 2007, Downey et al. 2010). The present study did not lend itself to ascertaining such diel-type effects on the sex-size class composition of commercial session-level chokka jig catches. However, Lipiński (1994) seemed to report strong selectivity for relatively large (28-33 cm ML) spawning-stage males with handline jigging trialled over an inshore spawning aggregation *during hours of darkness* on 11 November 1993; although it seemed unclear whether chokka were actively spawning when the jigging reported on was carried out, in which case it would make sense for larger-sized males to dominate catches following discussions above. That is why it seemed premature to conclude such overrepresentation across the commercial fishery in the present day (Lipiński 1994)[16]. Meaning it may be informative to investigate catch sex-size composition as a function of session-level variables such as diel period, austral season, location and location water depth, to answer if and when-where contemporary commercial chokka jigging may entail a least

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[16] There appeared to be grounds for arguing an overrepresentation of large (male) squid in nighttime jig samples collected from the DFFE *Algoa* research vessel over active spawning sites in 27-30 m deep waters in Kromme Bay, Eastern Cape in November (Lipiński 1994).

amount of bias as a fisheries-dependent source of biological parameter data (Lipiński 1994, Durholtz and Glazer 2022, Brandão and Butterworth 2024)[17].

Commercial chokka jig operators are presumed to seasonally vary in their day vs night allocations of effort (Githaiga-Mwicigi 2023). Sauer et al. (1992) seemed to indicate that, during peak-spawn (October-December) periods on the Plettenberg Bay-Port Alfred inshore, squids are mostly caught at daytime in ≤50 m deep waters, over aggregations of actively spawning squid. Further, within this same region, in late autumn to early spring (May-September), Schön (2000) seemed to observe a tendency of vessels allocating a greater proportion of within-season effort to nighttime operations 'offshore' (i.e., in waters 50-70 m deep – noted in preceding sections), due to encountering relatively greater CPUEs during such time periods in such areas on the fishing grounds. It therefore seemed plausible to expect an overall daytime decrease and nighttime increase in aggregate chokka abundance for mid-year periods.

The current study results, however, seemed to instead allude to overall chokka CPUE 'abundance' being relatively greater during daytime while remaining relatively low during nighttime for April-June periods (See Figure 19, Figure 20, Figure E2). This seemed to involve an intra-seasonal pattern of weak multimodal, less-than-spring/summer surges in daytime CPUE, at least within the context of modelling data employed in this study (See Figure 19, Figure 20, Figure E2). In other words, while adult chokka appeared to mostly aggregate at daytime in mid-spring to early summer (Oct-Dec), there seemed to also be a mid-year pattern of lesser, inconsistent increases in daytime chokka CPUE 'abundance' across the fishing grounds between 20-29°E (See Figure 19, Figure 20, Figure E2). In turn, this seemed to allude that any seasonal increases in vessels' nighttime – offshore operations are driven by factors additional to potential encounters of greater-than-daytime – greater-than-inshore CPUEs (Schön 2000). As skippers strive to at least avoid consistently operating at a commercial deficit barring suspension of operations, it was postulated there may be increased incidence and

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[17] "Little information exists regarding the male versus female ratio in the [chokka] squid catch. This needs further investigation…" (Durholtz and Glazer 2022, p. 7).

duration of nighttime sessions further offshore with, *inter alia*, notably less-than-spring/summer availability of chokka during daytime periods on the inshore. Meaning simply that vessels tend to target feeding squid in offshore waters when no squid are found inshore.

6.3 Is there spatial variation in any effects of diel period on chokka CPUE between seasons and years?

Results from this study support notions that spatial-temporal complexity is integral to the aggregative ecology of adult chokka on the South African south-southeast coast (See Chapter 1).

Current or imminent spawning-stage individuals are presumed able to optimally succeed in navigating the dynamic complexity inherent to sites' spatial-temporal suitability for, *inter alia*, nighttime feeding – daytime spawning (Barange 1994, Hanlon and Messenger 2018, Birch et al. 2020, Carter et al. 2022). This arguably leads to (1) the formation – break-up of aggregations fundamentally involving individuals' similar and, or synchronous response to environmental stimuli**[18]**; and (2) such site-specific ecological dynamics partly driving variation in the distributive abundance of aggregated adult squid across multiple sites in each of multiple areas (Schön et al. 2002, Sharma and Chandrashekaran 2005, Rodhouse et al. 2014, Hanlon and Messenger 2018, Birch et al. 2020). Hence, spatial-temporal estimates of chokka jig CPUE 'abundance' should ideally be interpreted in terms of broad as well as finer-detailed patterns while paying heed to relevant study drawbacks.

Caution needed to be taken when interpreting results with regard to spatial-temporal trends/patterns in chokka jig CPUE and associated aggregative squid behaviours, especially at finer-grained spatial-temporal scales. *Inter alia*, model approximations were informed by data arguably sub-optimal in terms of spatial resolution (i.e., at fishing grid cell scale), and lacking

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[18] Hypothetical examples may presumably include co-occurrent adult squid becoming more alert and receptive to reproductive opportunity at an individual level – initiating and, or responding to courtship/agonistic/mating behaviour – following a decrease in water turbidity when-where conditions are otherwise conducive and favourable to aggregative spawning (Schön et al. 2002, Sharma and Chandrashekaran 2005, Rodhouse et al. 2014, Hanlon and Messenger 2018, Birch et al. 2020).

in situ session-level measurements for notably relevant environmental parameters (e.g., bottom turbidity and sea surface-bottom temperature gradients). In addition, it should be kept in mind that these results largely pertained to the average year, a measure of central tendency in model estimates of day/night CPUE per day-of-year per Fishing grid cell across years. Arguable drawbacks to such an approach include neglect of any extraordinary CPUE estimations specific to a grid cell on a specific day of a specific year. Regardless of these shortcomings, however, relevant results allowed for qualitative assessment of where-when CPUE 'abundance' tended to be more or less on the modelled squid jig fishing grounds within the average year, while keeping the task of interpretation relatively simple.

Results seemed to partly allude to potential ways in which within-day/night and between-day/night adult chokka aggregations vary as a concomitant consequence of inshore-offshore – alongshore variability in the study area oceanography (See Figure 5, Multimedia 1, Figure 21). Overall, nighttime CPUEs appeared to be less than daytime CPUEs across most of the fishing grounds – for most of the average year. Although such a broad trend seemed to be expected following earlier discussions, it appeared surprising (1) inshore-offshore between Mossel Bay and Tsitsikamma National Park (~22-24°E); and (2) offshore, South-southeast off the coast of East London (~33.5-34.5°S – ~27.5-29°E) (See Multimedia 1).

As there appeared to be associations between adult loliginid feeding/abundance and favourably productive, cold, nutrient-rich waters (Gasalla et al. 2010, Jebri et al. 2022, Suca et al. 2022), these two regions were postulated to influence aggregative chokka ecology as seasonal and, or episodic centres of upwelling-related resources (e.g., primary ocean productivity). The inshore-offshore between Mossel Bay and Tsitsikamma National Park (~22-24°E) seemed to comprise of areas where the productive "Cold Ridge" and copepod maximum partly prevail when present on the Agulhas Bank (Roberts 2005, Jacobs et al. 2022b, Hancke et al. 2023, Huggett et al. 2023). In comparison, areas offshore, South-southeast off the coast of East London (~33.5-34.5°S – ~27.5-29°E) appeared to constitute a relative origin for intermittent, meander-driven upwelling adjacent to the shelf-edge of the far Eastern Agulhas Bank (Goschen et al. 2015, Malan et al. 2018). Hence, on the premise that most adult chokka are naturally inclined to feed as and when sustenance is available, mostly in the offshore and preferably at night (Sauer and Lipiński 1991, Sauer et al. 1992), results were expected to allude to squids' intermittent nighttime preference rather than seeming annual persistence of greater daytime CPUE ‘abundances’ in areas encompassed in these two regions (See Multimedia 1). Alternative possibilities seemed to arguably include:

1. predominant nighttime avoidance of offshore areas with narrowing in the continental shelf (e.g., ~33.5-34.5°S – ~27.5-29°E; See Multimedia 1, Figure 21), considering chokka are mostly found at ≤200 m bathymetries, adjacent inshore of the continental slope on the south-southeast coast (See Chapter 1); and, or
2. an actual intermittent nighttime preference for these areas while indications of overall daytime CPUE prominence are, *inter alia*, an artefact of previously mentioned study drawbacks.

However, it is outside the purview of this study to deterministically establish validity of these courses of reasoning, and validation therefore requires looking to other sources of evidence. Previous pertinent research seemed to have largely involved studying the abovementioned regions (i.e., (1) ~22-24°E and (2) ~33.5-34.5°S – ~27.5-29°E) in contexts of relationships between chokka spawner to population/fishery recruitment success and fluxes in biophysical-biochemical processes on and adjacent to the Agulhas Bank (e. g., Roberts and van den Berg 2002, Roberts 2005, Carter et al. 2022). It therefore seems advisable for future endeavours to involve *in situ* investigations of day/night adult chokka abundance specifically in Mossel Bay-Tsitsikamma National Park areas and areas offshore of East London, within contexts of potentially larger-scaled – longer-timed peaks and troughs in ocean productivity. Such investigation would arguably allow for a more thorough and detailed account of squids’ actual diel-type use of these regions, in terms of complex patchiness inherent to these environments’ spatial-temporal suitability as, *inter alia*, nighttime feeding and, or daytime spawning grounds.

Spatial-temporal results seemed to also allude to a Jan-Mar and Jul tendency for higher nighttime CPUEs to manifest in:

- the Tsitsikamma National Park-Algoa Bay offshore (24-26°E), particularly in shelf-edge vicinities of the 200 m isobath – a region seemingly characterised, in part, by intermittent shelf-edge upwelling consequent to shelf-edge current shear and, or shear-related after-effects (e.g., shear-edge sub/mesoscale cyclonic eddies and attendant warm surface water plumes) (Goschen and Schumann 1988, Lutjeharms et al. 1989, Lutjeharms et al. 2003, Tedesco et al. 2019); and

- the Cape Agulhas-Cape Infanta inshore-offshore (20-21°E), particularly in the mid-shelf vicinity of the Alphard Bank (~35°S, ~20.5-21°E) – a region seemingly partly characterised by east to northeast mid-shelf intrusion of waters upwelled via divergent surface currents west-southwest of the Alphard Bank ridge (~35°S, ~20.5°E) (Shannon and Chapman 1983, Chapman and Largier 1989, Lutjeharms et al. 1996) (See Multimedia 1).

Hence, there may potentially be some degree of correspondence between near-seasonal peaks in nighttime chokka CPUE 'abundance' and upwelling-related ocean productivity within these regions. Also, such mechanisms of oceanic biological production are seemingly more pronounced in effect during austral summer periods – when there is increased duration-intensity-prevalence of surface layer insolation, upwelling-favourable easterly winds and associated increases in current velocities (Hutchings 1994, Jury 1994, Lutjeharms et al. 1996, Tedesco et al. 2019, Jury 2020). Considering relevant peaks in nighttime CPUE also mostly appeared greater in Jan-Mar (mid-summer to early autumn) than Jul (winter) (See Multimedia 1), results seemed to further support notions that, within these regional fringes of the Plettenberg Bay-Port Alfred inshore, adult chokka are notably attuned in their nighttime feeding habits to relative peaks in ocean productivity.

Chapter 7: Conclusions

This study helps to inform the squid-dedicated, *L. reynaudii* (chokka) acoustic survey programme developed and deployed on the South African southeast coast since 2019. In particular, it helps clarify the validity of understandings around when-where adult chokka may tend to form acoustically detectable aggregations in South African waters throughout the year.

The study investigated spatial-temporal diel-type variations in chokka catch rates and the associated aggregated proportion of adult chokka on the commercial squid jig fishing grounds of South Africa. Essentially, the rationale was to ascertain whether there is a match between the spatial-temporal focus of hydroacoustic surveys (i.e., mainly: Plettenberg Bay-Port Alfred areas at daytime during October-November); and when-where adult squid mostly aggregate throughout the year according to the large, long-term body of available DFFE chokka jig catch data.

A semi-parametric generalized additive modelling approach was taken to analyse Catch Per Unit Effort (CPUE) in DFFE records of commercial session-level squid jig logbook catch data for 2006-2022. Assuming *standardised* CPUE to be a representative measure of local chokka abundance and proportional representation of regional population distribution, modelling was done to adequately account for data non-linearity and non-normality when estimating relevant predictors' marginal effects, to answer:

1. Is there an effect of diel period on chokka CPUE on the commercial squid jig fishing grounds of South Africa?
2. Is there seasonal variation in any effects of diel period on chokka CPUE on the commercial squid jig fishing grounds of South Africa?
3. Is there spatial variation in any effects of diel period on chokka CPUE between seasons and years on the commercial squid jig fishing grounds of South Africa?

The aggregated proportion was greater at day than night (See Figure 18); and remained relatively constant throughout the year except in mid-spring to early summer (October-December), and (to a much lesser, and less obvious extent) in autumn/winter (April-June), when the daytime CPUE was much greater (See Figure 19, Figure 20, Figure E2). It would be worth calculating the average aggregated proportion in these two periods, averaged over each month and the whole of each seasonal time series.

Given continued debate on whether there is tendency for a minor spawning peak in Autumn, it was also interesting to note modelling evidence of minor peaks in April-June CPUE (See Figure 19, Figure 20). However, such a finding is best interpreted tentatively when deliberating on present-day chokka spawning patterns, considering 2013 was the last year modelling data was fully complete for these periods (See Chapter 1, Chapter 2).

Diel-seasonal CPUE variations also demonstrated spatially complex linkages between aggregative chokka ecology and oceanography of the South African Agulhas Bank region (See Chapter 5, Chapter 6). Involving greater daytime CPUEs across most of the modelled fishing grounds for most of the average year (See Chapter 5), such complexity was to be expected considering the social-ecological nature of a species such as chokka squid (See Chapter 1). However, it was interesting to infer season-type associations (or a lack of such associations) between greater nighttime CPUEs and upwelling-related ocean productivity, in areas peripheral to the main Plettenberg Bay-Port Alfred inshore fishing/spawning grounds (See Chapter 5, Chapter 6). However, there is a need for caution in making inferences regarding associations between the aggregated proportion and parameters of physical-chemical oceanography based on the present study’s findings, considering the modelling data did not include measurements of oceanographic variables concomitant to session-level variations in CPUE (e.g., primary production). Therefore, it is also recommended for there to be an account of relevant oceanographic parameters as part of future endeavours to explain and investigate session-level, diel-type variations in CPUE.

To conclude, the evidence here largely supports focussing aggregate-dependent survey efforts on daytime October-November periods between Plettenberg Bay and Port Alfred, to achieve a relative measure of the South African adult chokka population during peak abundance periods. Meaning the study has not revealed any new pronounced diel, seasonal or spatial trends in the aggregated proportion– a useful finding in itself given the previous lack of research on this spatial and temporal scale. Hence, the study makes a contribution to the development of the acoustic survey programme (the rationale for the project) in that it dismisses any notion that large, acoustically-surveyable aggregations of squid are likely to be found consistently in areas and at times other than the area currently being surveyed acoustically at daytime in late spring (cf. Section 1.4). This will at the least set some limits on future hypotheses about spatial and temporal dynamics in the aggregated proportion of the adult chokka squid population in South African waters.

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Appendices

Figure A1: Diagnostic plot of deviance residuals against jigging session duration per diel period.

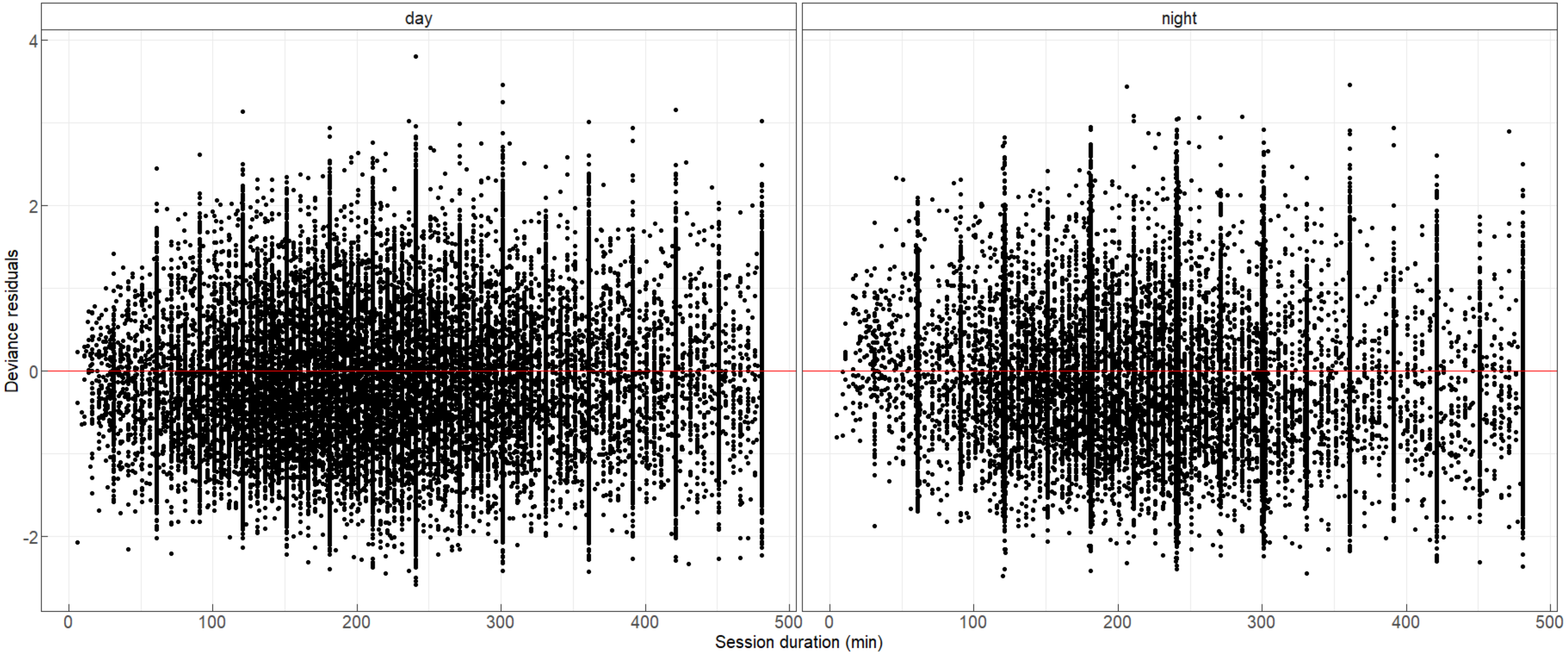

Figure A2: Diagnostic plot of deviance residuals against jigging session reported water depth per diel period.

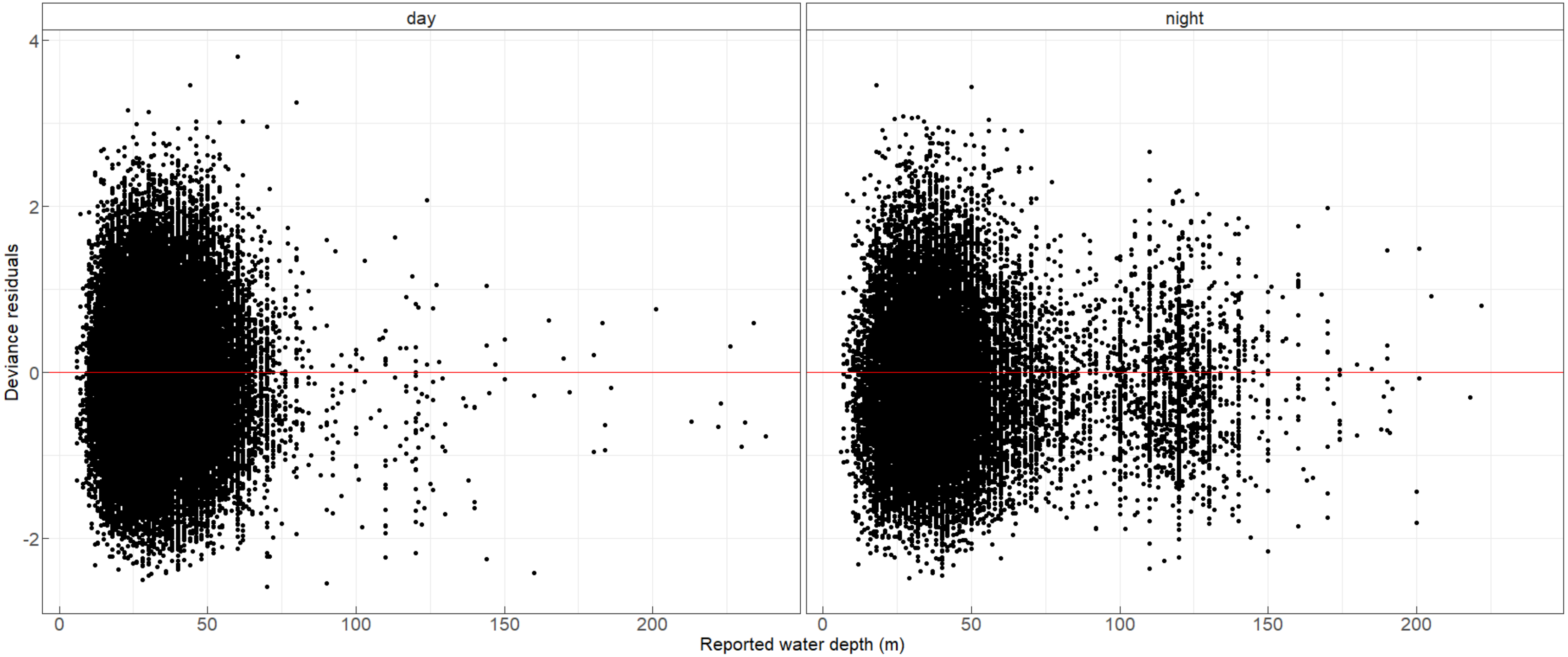

Figure B1: Map of deviance residuals by month per diel period.

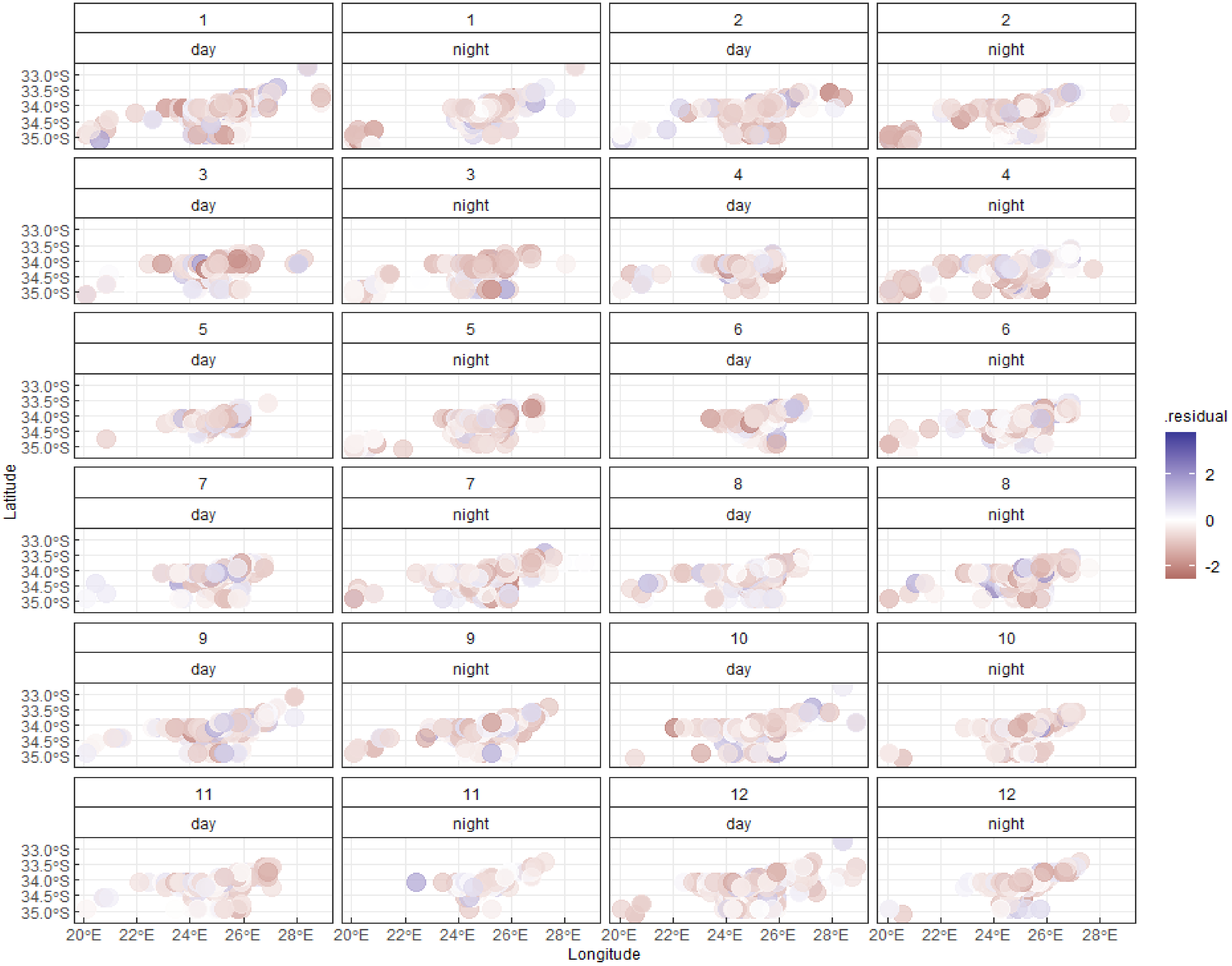

Figure B2: Map of deviance residuals by year per diel period.

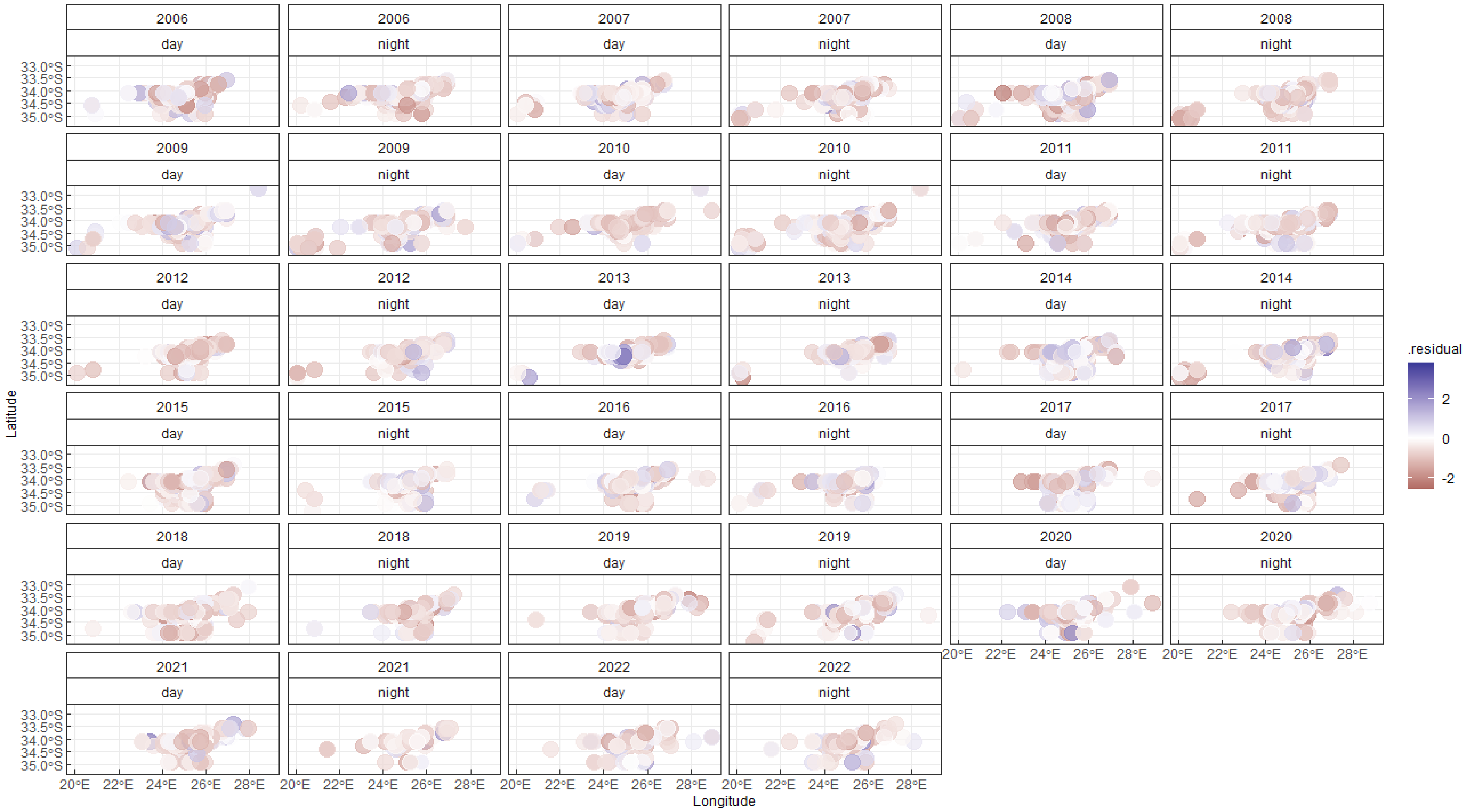

Figure C1: Overall concurvity of model terms: "worst" constitutes an overestimation of covariate concurvity, "observed" potentially constitutes an underestimation of covariate concurvity, and "estimate" arguably constitutes a relatively realistic estimation of covariate concurvity (Wood 2023, Simpson 2024).

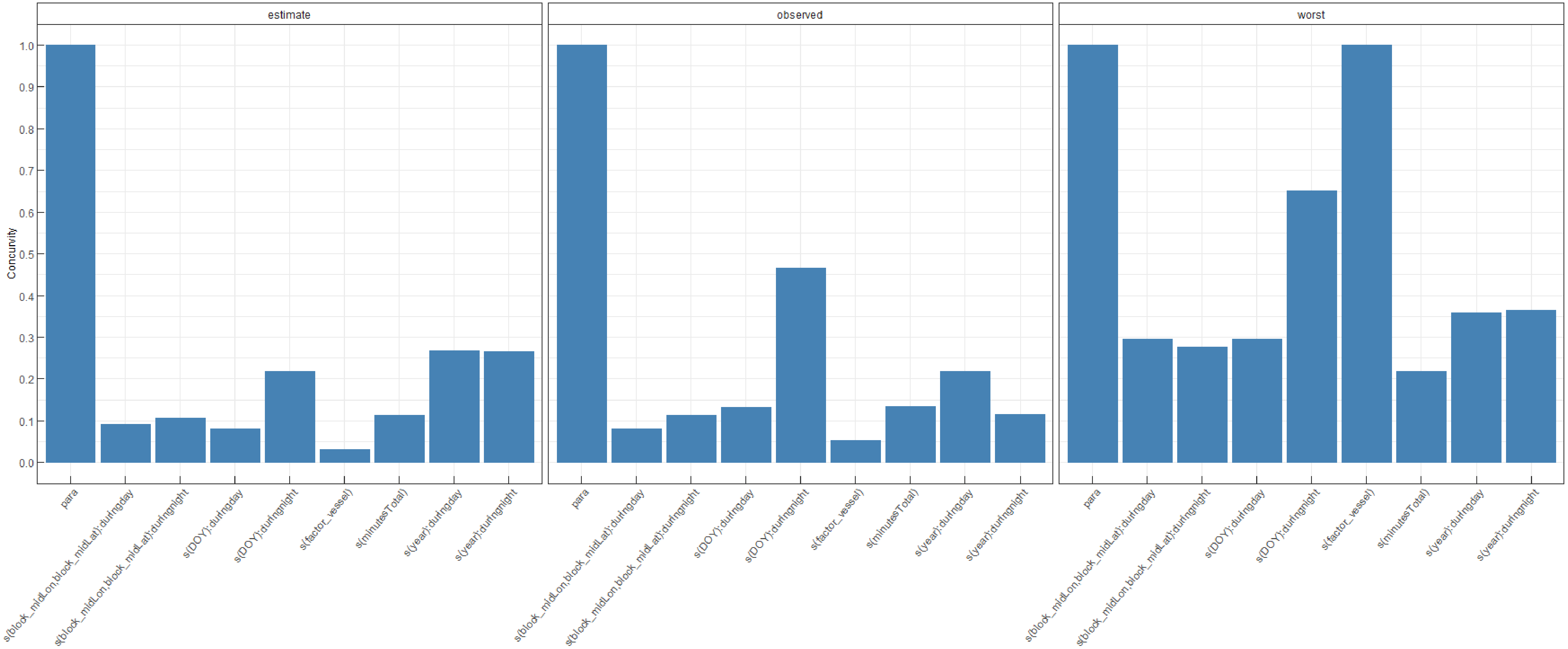

Figure C2: **Smooth-wise partitioning of model terms' concurvity: "worst" constitutes an overestimation of covariate concurvity, "observed" potentially constitutes an underestimation of covariate concurvity, and "estimate" arguably constitutes a relatively realistic estimation of covariate concurvity (Wood 2023, Simpson 2024).**

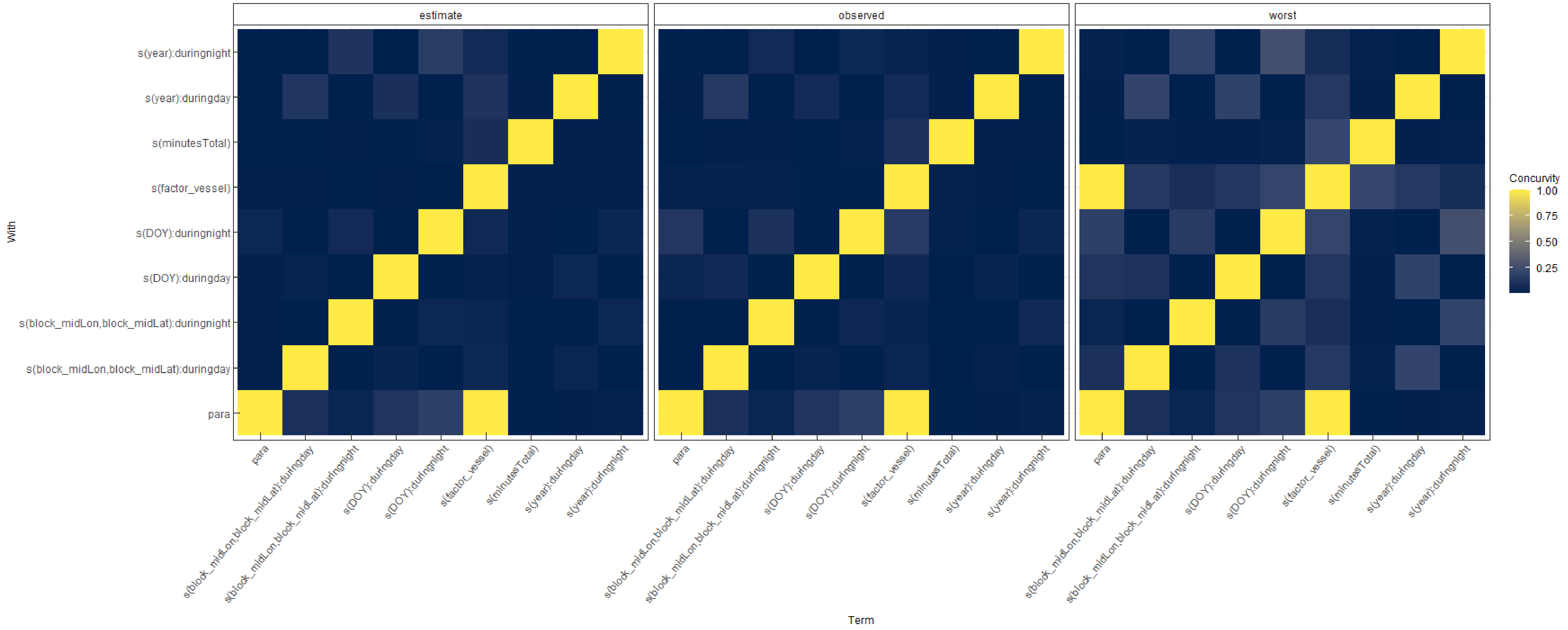

Figure D1: **Model residual boxplots per diel period, by month. Red horizontal lines denote [0.5; -0.5], a range in which residuals are fairly low in their deviance from zero.**

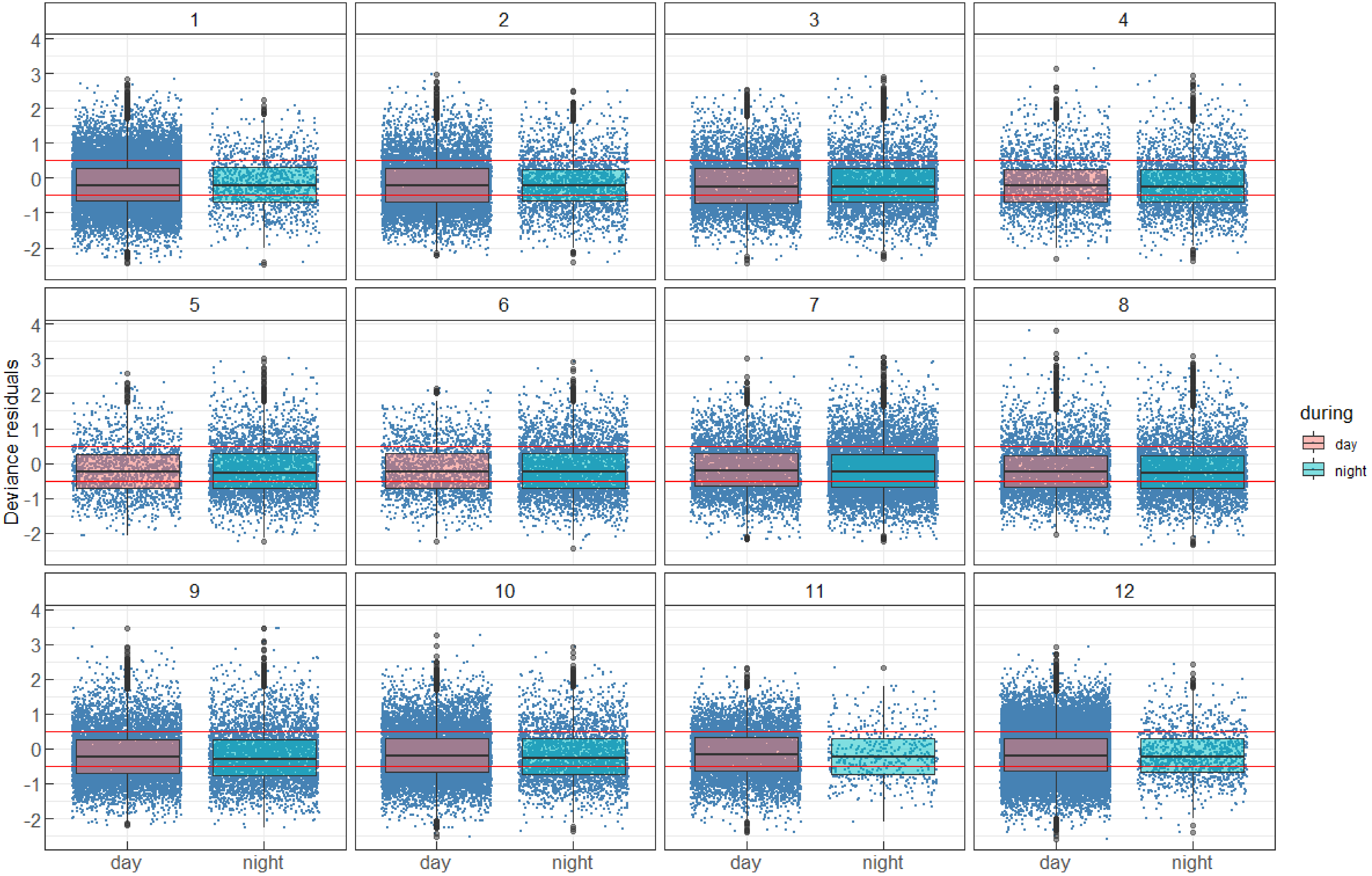

Figure D2: **Model residual boxplots per diel period, by year. Red horizontal lines denote [0.5; -0.5], a range in which residuals are fairly low in their deviance from zero.**

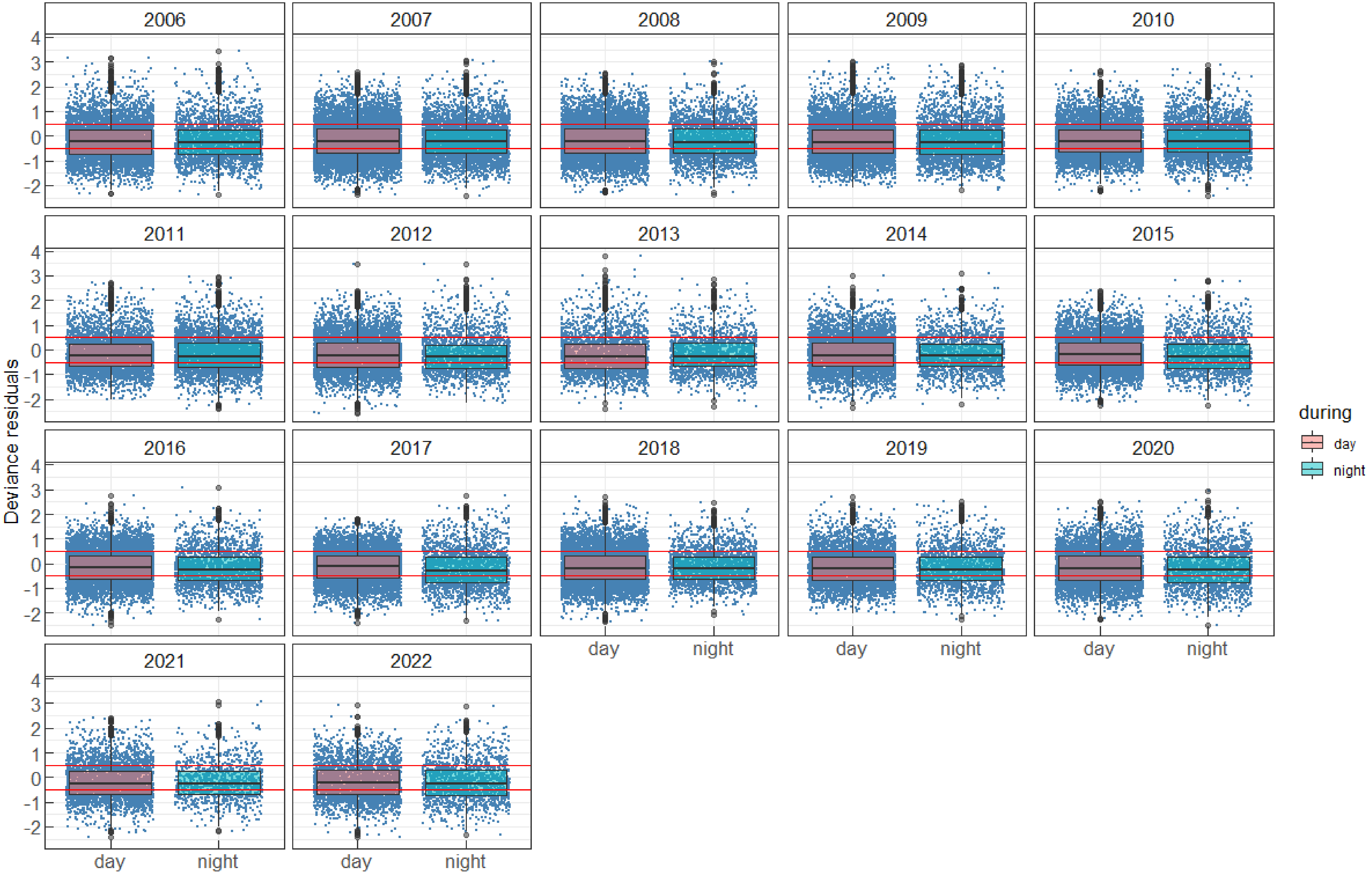

Figure E1: ***A posteriori*** **investigation of the raw 2006-2022 modelling data, regarding count of day/night sessions reportedly carried out per interval of jigging location water depth: a) overall and b) according to month.**

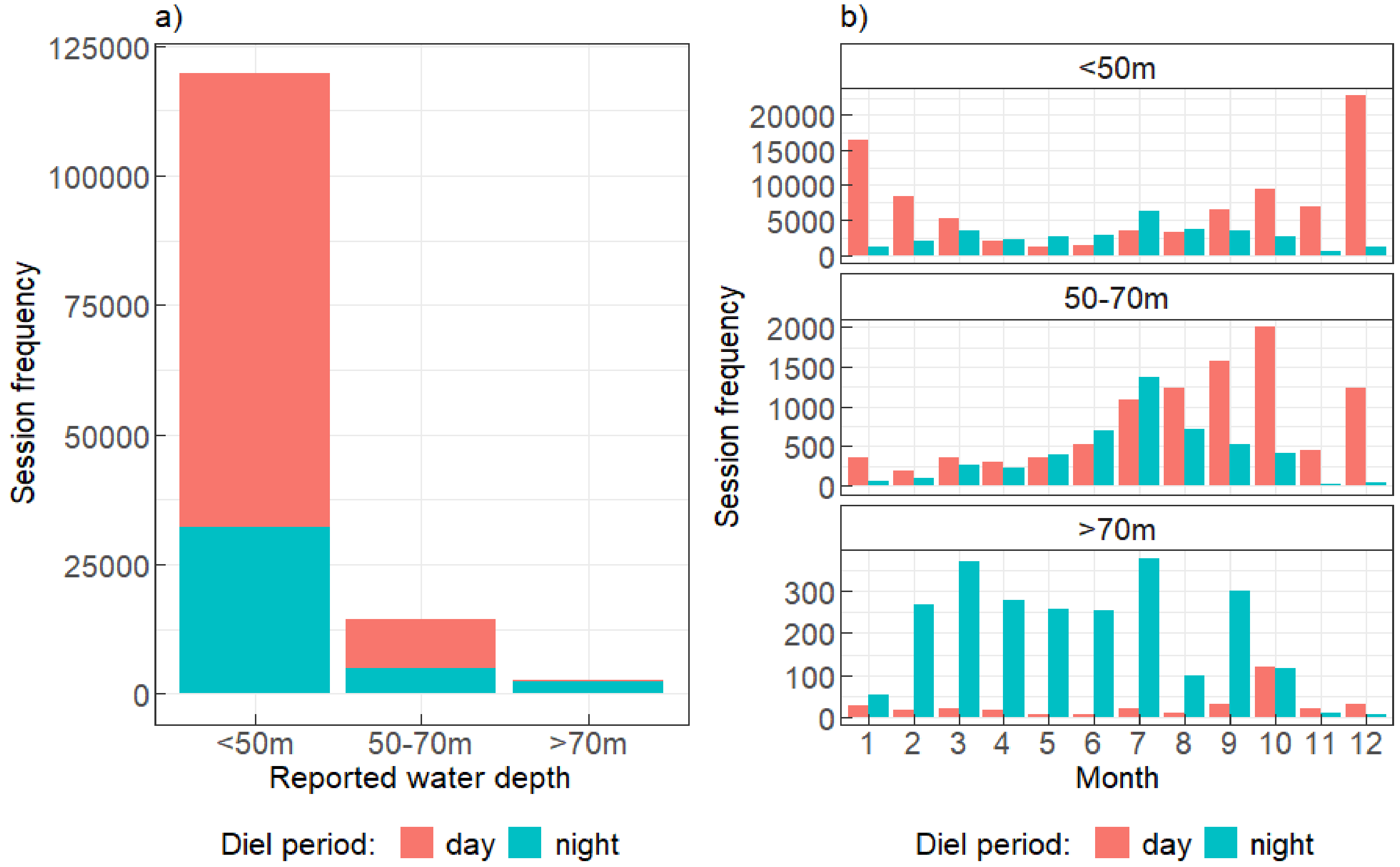

Figure E2: Log of the combined marginal effect of day-of-year and diel period with day/night plotted together without confidence bands. The x-axis shows day-of-year at a monthly interval after converting to date.