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Spatio-temporal dynamics in maturation and spawning of Patagonian toothfish *Dissostichus eleginoides* on the sub-Antarctic Kerguelen Plateau

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This study investigated maturation and spawning of Patagonian toothfish *Dissostichus eleginoides* in the Heard Island and McDonald Islands (HIMI) fishery on the Kerguelen Plateau in the Indian Sector of the Southern Ocean based on gonads and otoliths collected between 2004 and 2015 and using histological analyses and calibration of macroscopic staging criteria. *Dissostichus eleginoides* at HIMI spawn throughout the austral late autumn and winter months of May–August and spawning activity is concentrated on slopes along the west and south of the plateau around HIMI at depths of 1500–1900 m. Comparison between histological analyses and macroscopic gonad staging indicated that many fish that had spawned, as indicated by the presence of post-ovulatory follicles, returned to a resting stage which was macroscopically indistinguishable from maturing fish. Furthermore, the occurrence of females of all size classes with low gonado-somatic index and low macroscopic gonad stage during the spawning season suggested that a proportion of mature females did not spawn every year. Age-at-maturity estimates, based on the assumption that fish of macroscopic stages ≥2 were mature, decreased between the 2004–2009 and 2010–2015 periods for both sexes. The magnitude of this temporal variation in age at maturity, however, varied between gear types and fishing depths and variable sampling regimes probably influenced these variations. This study highlights the importance of correct interpretation of macroscopic gonad stages and understanding the influence of fishery operations on estimations of life-history parameters.

Key words: Nototheniidae; oocyte; reproduction; Southern Ocean; spermatozoa; stock assessment.

INTRODUCTION

Life-history traits such as growth, natural mortality and age at maturity are some of the primary determinants of population dynamics, stock biomass and stock demography (Jørgensen *et al.*, 2007). Sustainable fisheries management requires reliable estimates of these traits and how they may vary in space and time. Spatial and temporal variations in age and size at maturity have been observed in many commercially-exploited fish stocks (Stokes & Law, 2000; Jørgensen *et al.*, 2007; Heino & Dieckmann, 2008). The

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presence of multiple confounded factors, however, complicates identification of the drivers of these changes in observational studies (Sharpe & Hendry, 2009). Changes in estimates relating to sexual maturity have been linked to temporal variation in environmental conditions such as water temperature (Cox & Hinch, 1997; Cardinale & Modin, 1999) and fishing pressure (Heino & Godø, 2002; Jørgensen *et al.*, 2007; Sharpe & Hendry, 2009). Life-history traits may also appear to be temporally variable if there is spatial structuring of these traits within the population and if sampling is not consistent in time and space (Sharpe & Hendry, 2009). Inconsistent sampling may be particularly prevalent when fishery-dependent data are used to estimate life-history traits of the harvested fish population and when fishery operations are dynamic over time with regard to fishing gears, gear selectivity, fishing locations and fishing depths.

Patagonian toothfish *D. eleginoides* Smitt 1898 (Perciformes, Nototheniidae) has a broad geographic distribution, mainly in waters around sub-Antarctic islands and as far north as 20° S in some regions (Gon & Heemstra, 1990; Eastman, 1993; Arkhipkin *et al.*, 2003). It is one of the most common demersal fish species in shelf and slope waters of the Kerguelen Plateau in the Indian Sector of the Southern Ocean (Fig. 1), which encompasses an Australian exclusive economic zone (EEZ) around Heard Island and the McDonald Islands (HIMI) and a French EEZ around the Kerguelen Islands (Williams & de la Mare, 1995; Duhamel & Hautecoeur, 2009). *Dissostichus eleginoides* occupy a broad depth range from 10 m to over 2500 m, with an ontogenetic habitat shift towards deeper waters as fish grow older (Agnew *et al.*, 1999; Arkhipkin *et al.*, 2003; López Abellán, 2005; Arkhipkin & Laptikhovsky, 2010; Péron *et al.*, 2016). As a result of this broad depth distribution, the Kerguelen Plateau represents a large expanse of contiguous habitat for *D. eleginoides* (Fig. 1).

Fishing for *D. eleginoides* at HIMI in the Australian EEZ started in 1997 as a trawl fishery operating in depths <1000 m and catching fish predominantly <800 mm total length (L_T). The use of longlines was introduced in 2003 and gradually increased in following years to be the current primary fishing method (Constable & Welsford, 2011; Péron *et al.*, 2016). The transition from trawl to longline fishing has allowed fishing across a broader range of depths and locations, thereby influencing the catch composition of *D. eleginoides* (Welsford *et al.*, 2009; Péron *et al.*, 2016).

Prior to 2009, *D. eleginoides* in spawning condition were rarely encountered in the HIMI fishery. In contrast, mature males and females were encountered in deep water (≥1000 m) on demersal longlines in the north-west of the French EEZ on the Kerguelen Plateau and in another French EEZ around Crozet Island (Fig. 1), with running-ripe fish being captured during July and August (Lord *et al.*, 2006; Duhamel *et al.*, 2011). This information, in combination with genetic, tagging and length-distribution data, led to the hypothesis that all recruits on the Kerguelen Plateau derive from spawning activity in the French EEZ, with significant implications for Australian and French management of these stocks (Williams *et al.*, 2003*b*). Between years 2009–2011, however, commercial longline fishing during winter in deep slope waters to the west of HIMI encountered substantial numbers of *D. eleginoides* in spawning condition (Welsford *et al.*, 2012*a*). These findings highlighted the need for an improved understanding of spatio-temporal dynamics in maturation and spawning of *D. eleginoides* on the Kerguelen Plateau.

Estimates of age at maturity for the current assessment model for *D. eleginoides* in the HIMI fishery have been based on length-at-maturity ogives that were translated to age at maturity at a time when little ageing data were available. A long-term

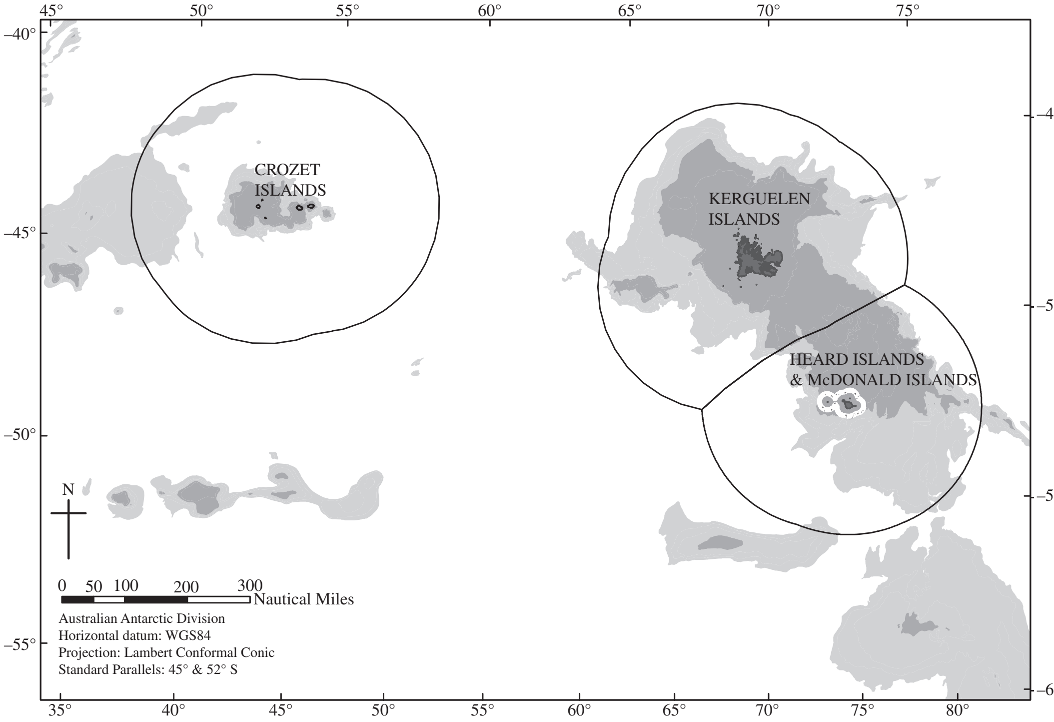

Fig. 1. Map of the main subantarctic island groups and Exclusive Economic Zones (EEZs) in the Indian Sector of the Southern Ocean including the Australian Heard Island and the McDonald Islands (HIMI), and the French Kerguelen Islands and Crozet Islands. The Kerguelen Plateau refers to the large area of elevated seafloor around HIMI and the Kerguelen Islands. Dark grey shading = 0–1000 m, light grey shading = 1000–2500 m, white fill = >2500 m, black lines = EEZ limits, white line = Territorial Sea Limit. Bathymetry data courtesy of the Australian Antarctic Data Centre.

ageing programme at HIMI, however, now provides the data for a direct approach that links gonad-stage and ageing data from fish otoliths (Welsford *et al.*, 2015). Accordingly, the aims of this study were to describe the size distribution and dynamics of *D. eleginoides* in spawning aggregations in the Australian EEZ at HIMI, refine sex-specific estimates of age at maturity and investigate temporal variation in these estimates.

MATERIALS AND METHODS

BIOLOGICAL DATA COLLECTION

The HIMI *D. eleginoides* fishery has had 100% scientific observer coverage of all hauls since it began in 1997. Biological data, collected from randomly sampled *D. eleginoides* from longline and trawl fishing events included L_T (mm), total mass (M, g), sex and macroscopic gonad stage. Fish lengths were measured using electronic fish measuring boards designed and built at the Australian Antarctic Division. Masses were recorded with motion-compensated scales (Unisystem Marine Scales; www.unisystem.se). Sex and macroscopic gonad stage were determined according to the scale in Kock & Kellermann (1991) (Table I). Gonad masses were also recorded from some fish (primarily during the winter of 2011), enabling calculation of gonado-somatic index (I_G; *i.e.* gonad mass as a proportion of total body mass) for those individuals. The geographic coordinates, times and depths were recorded at setting and hauling of

TABLE I. Criteria and stages used for macroscopic assessment of gonad development of *Dissostichus* spp. (Based on Kock & Kellermann, 1991)

Female			Male	
Stage	Status	Appearance	Status	Appearance
1	Immature	Small, firm, pink–translucent, no eggs visible to naked eye.	Immature	Small, whitish, narrow strips lying close to the vertebral column.
2	Maturing virgin or resting	More extended, firm, small oocytes visible, giving ovary a grainy appearance.	Developing or resting	White, flat, convoluted easily visible to the naked eye, about $^1/_4$ length of the body cavity.
3	Developing	Large, starting to fill the body cavity, contains yellow-orange oocytes of two sizes.	Developed	Large, white and convoluted, no milt produced when pressed or cut.
4	Gravid	Large, filling or swelling the body cavity, when opened large ova spill out.	Ripe	Large, opalescent white, drops of milt produced when pressed or cut.
5	Spent	Shrunken, flaccid, contains a few residual eggs and small ova.	Spent	Shrunk, flabby, dirty white in colour.

each fishing event. Length and mass data were collected from 619 870 *D. eleginoides*, of which 12 932 also had sex, macroscopic gonad stage and gonad mass recorded (Table S1, Supporting information).

GONAD SAMPLE COLLECTION AND HISTOLOGICAL ANALYSES

Histology samples were collected during a winter (June–September) 2011 longlining voyage that included sampling across a large area of the deep slope to the north-west, west and south of Heard Island and McDonald Islands (Welsford *et al.*, 2012*a*). Gonads were excised whole, weighed to the nearest gram, cut into sections of 3–7 g and preserved in 10% FAACC (formaldehyde 4%, acetic acid 5%, calcium chloride 1·3%) in seawater. On return to Australia, samples were transferred to 10% ethanol prior to histological processing. A total of 197 female and 75 male gonads were suitable for histological analysis (Tables II and III).

A sub-sample from each gonad was enclosed in a tissue cassette, mounted in paraffin wax, sliced using a microtome into *c.* 6 μm sections and stained using a standard haematoxylin and eosin procedure. Sections were viewed and photographed under a microscope (×10 to ×400) to identify and categorize the developmental stages of gametocytes.

Cell categorization and histological maturity staging were determined according to descriptions by West (1990), Ewing & Lyle (2009) and Murua *et al.* (2003). Microscopic maturity was classified for each sample by the most advanced type of oocyte (West, 1990) or cell type in sperm development (Parker & Grimes, 2010) that was present. Presence of post-ovulatory follicles (POFs), oocyte atresia and residual eggs were also recorded. For male gonad histology, maturity was determined by the development stage of spermatocytes and the general microscopic morphology of the gonad.

POFs are the remaining follicular structure that surrounds the ovum prior to their release (Saidapur, 1982). In teleosts, POFs are visible in the ovary after spawning, thus their presence constitutes evidence that an individual is mature and has spawned in the past. As POFs begin to deteriorate, however, it can become difficult to differentiate between POFs and atretic oocytes and this may lead to incorrect identification of fish that have spawned as opposed to fish that

TABLE II. Comparison of macroscopic staging of female *Dissostichus eleginoides* ovaries with oocyte stage present in histological sections, *e.g.* for stage 1 early perinucleolus were present in 100% of all sections, whereas late perinucleolus were only present in 72% of all sections. Shaded cells indicate the most advanced oocyte stages expected given the assigned macroscopic stage is accurate, *e.g.* the presence of cortical alveoli indicates stage ≥2, and individuals assigned to stage 2 should not contain oocytes further advanced than late vitellogenesis stage. *n.b.* Varied combinations of oocytes– post–ovulatory follicles (POF) types in sections mean that percentages cannot be summed together, *e.g.* the sum of non–shaded values under stage 1 ≠ the percentage of individuals incorrectly staged

	Assigned macroscopic maturity stage (%)				
Oocytes types–POFs present	Stage 1 (*n* = 46)	Stage 2 (*n* = 48)	Stage 3 (*n* = 75)	Stage 4 (*n* = 7)	Stage 5 (*n* = 21)
Early perinucleolus	100	100	100	100	100
Late perinucleolus	72	98	100	100	100
Cortical alveoli	26	96	100	100	100
Early vitellogenesis	4	17	48	57	52
Mid vitellogenesis	–	27	39	29	67
Late vitellogenesis	–	10	9	29	14
Early migratory nucleus	–	–	55	–	–
Late migratory nucleus	–	–	87	57	–
Post migratory nucleus	–	–	25	57	–
Hydrated	–	–	7	57	–
Residual hydrated	–	–	–	–	52
Recent POFs	–	4	5	57	95
Old POFs	4	27	4	–	–
Atresia	–	19	13	14	24
Old Atresia	9	60	4	–	5
Unknown	2	35	1	–	5
Only lower–stage cells[a] and no indicators of spawning or oocyte development[b] present	0	4	0	14	5
Macroscopic stage = microscopic stage	74	94	92	57	95
Higher–stage cells[a] or indicators of spawning or oocyte development[b] also present	26	65	20	43	95

[a] Lower-stage and higher-stage cells refer to those above or below, respectively, the shaded cells under each macroscopic maturity stage.

[b] Indicators of spawning or oocyte development include recent POF, old POF, atresia, or old atresia.

have arrested egg development prior to spawning (Ganias, 2011). For the purposes of this study, POFs were assumed to be readily identifiable because the majority of samples were from fish sampled within a few months of the predicted spawning season and because POFs in the closely related Antarctic toothfish *Dissostichus mawsoni* Norman 1937 were shown to persist for several months post spawning (Parker & Grimes, 2010). Structures with traits of both POFs and atretic oocytes were recorded as unknown in order to minimize false identification of POFs (Tables II and III, Supporting information).

TABLE III. Comparison of macroscopic staging of male *Dissostichus eleginoides* testes with spermatozoan development evident in histology sections. Shaded cells indicate cells that are expected to be present in a maturity stage. Shaded cells indicate the most advanced cell stages expected given that the assigned macroscopic stage is accurate, *e.g.* individuals assigned to stage 1 should not contain cells further advanced than the spermatogonium stage

	Assigned macroscopic maturity stage (%)				
Cell-structures present	Stage 1 (*n* = 17)	Stage 2 (*n* = 13)	Stage 3 (*n* = 15)	Stage 4 (*n* = 16)	Stage 5 (*n* = 13)
Spermatogonia	94	77	27	19	77
Spermatids	6	23	100	94	69
Spermatozoa	–	–	60	81	62
Open lumen	–	–	13	13	77
Individuals correctly staged	94	23[a]	40[a]	81	77

[a] Percentages of macroscopic stage 2 and 3 fish, respectively, that were microscopic stage 2–3. Microscopic staging could not distinguish between stages 2 and 3.

PROCESSING AND AGEING OF OTOLITHS

The sagittal otoliths were collected from five fish in each 10 mm length bin across the length range of fish captured during each voyage. One otolith was selected at random for each fish and embedded in clear epoxy resin. Three 350 μm sections were taken transversely in the vicinity of the primordium using a Buehler Isomet low-speed saw (www.buehler.co.uk). Sections were polished using 12 μm lapping film and mounted onto slides using polyester casting resin (98% resin and 2% methyl ethyl ketone peroxide catalyst). Images of sectioned otoliths were taken using a Leica MZ95 microscope, Leica DFC450 camera and the Leica application suite software (www.leica.com). Age was estimated from these images by counting the incremental opaque zones, which have been shown to form annually in *D. eleginoides* otoliths (Kalish & Timmiss, 1997). Each otolith was aged by at least two experienced readers. Methods of reader training, cross validation and quality control are described in Welsford *et al.*, (2012*b*) and Farmer *et al.*, (2014). A reference collection of otolith images is a key component of the quality control procedure and is used to assess levels of precision and bias for an individual reader against consensus-derived ages for the reference otoliths over time. The reference collection is read three times annually, at which times precision and bias is also assessed between the two independent readers. During the present study, precision was invariably found to be within acceptable bounds (index of average per cent error, IAPE <5%) with no significant bias detected between any reader and the reference collection, or between any pair of readers (Welsford *et al.*, 2012*b*; Farmer *et al.*, 2014). For fish with multiple age estimates, the median of the estimates was used, with decimal places being rounded either up or down at random for each fish.

ESTIMATION OF AGE AT MATURITY

For all individuals with age and gonad-stage data, age estimates were assigned to single-year bins and individuals were classified as either immature or mature. Age-at-maturity ogives were fitted assuming that either gonad stages ≥2 were mature or that stages ≥3 were mature. Fish sampled prior to 2004 and outside of the main spawning season of May–August were excluded. Age at 50% maturity (A_{50}) was estimated for males and females separately and for both sexes pooled. To investigate temporal variation in maturation, data were also split into two time periods for separate analyses: years 2004–2009 and 2010–2015. Only two time periods were compared to ensure sufficient age data in each period. Data exploration included inspection of histograms of ages for each combination of maturity stage, sex and time period to check for outliers and sufficient observations within each factor-level combination. For each combination of sex and time period, a single logistic regression model (stats package in R; www.r-project.org) was applied with the natural logarithm of the odds of an individual being mature (*i.e.* logit link) as a linear function of the explanatory variable, age, where maturity was assumed to follow a Bernoulli distribution. Non-parametric bootstraps with 10 000 iterations were used to calculate confidence intervals. Relationships between age and variables other than maturity stage were investigated using pairwise scatter-plots.

RESULTS

Length-frequency distributions varied between gear types. Trawl-caught fish were generally <800 mm L_T and longline-caught fish were predominantly 600–1200 mm (Fig. S1, Supporting information). While the sex ratio was *c.* 1:1 for smaller size classes, the proportion of males in the catches rapidly declined above 1000 mm and few males >1600 mm were observed in samples (Fig. S1, Supporting information).

HISTOLOGICAL *V.* MACROSCOPIC GONAD STAGING

Histological sections from female *D. eleginoides* showed tissue cell structures typical of those described for other teleost fishes (West, 1990; Murua *et al.*, 2003; Ewing & Lyle, 2009), enabling the characterization of 11 distinct stages of oocyte development (Fig. S2 and Table S2, Supporting information). Atretic oocytes and two age classes of POFs were also identified (Fig. S3 and Table S3, Supporting information).

The histology of male gonads enabled classification into four distinct stages based on the appearance of cells dividing to produce spermatozoa development and testis morphology (Fig. S4 and Table S4, Supporting information). No clear cellular or tissue structures were identified that enabled a clear distinction to be drawn between developing fish in stages 2 and 3.

For females, macroscopic gonad staging successfully categorized individuals into the correct cellular developmental stage (*i.e.* the histological stage) for 94% of individuals in stage 2, 92% of individuals in stage 3 and 95% of individuals in stage 5 (Table II). Nevertheless, 65% of macroscopic stage 2 fish contained either recent POFs, old POFs, atresia or old atresia; indicating they were likely to be individuals that had spawned at some time in the past, or that oocyte development had commenced in the past and been arrested. These indicators of previous spawning suggest that a majority of stage 2 fish should be considered to be mature when estimating age at maturity. Agreement between staging methods was lower for females of macroscopic stage 1 (74%), with 26% of those individuals revealed to have more-advanced stages of oocyte development and histological characteristics of maturity in the form of old POFs and atretic oocytes.

Misclassification of macroscopic stage 3 females included some stage 4 fish as determined by the presence of hydrated oocytes and one stage 5 fish with recent POFs. Only seven of the individuals assessed as macroscopic stage 4 were collected at sea and while 57% were correctly staged, histological analysis indicated that one was a misclassified stage 3, with no hydrated oocytes evident, but post-migratory nucleus-stage oocytes present and two were misclassified stage 5 fish with recent POFs, but no hydrated oocytes present. Macroscopic classification of stage 5 (spent) females had a very high classification success, with 95% of specimens including recent POFs. Only one macroscopic stage 5 individual could not be classified due to the absence of POFs and the presence of ambiguous structures. Taken together, unlike for stages 1 and 2, the misclassification of macroscopic stages 3, 4 and 5 is not expected to bias A_{50} estimates

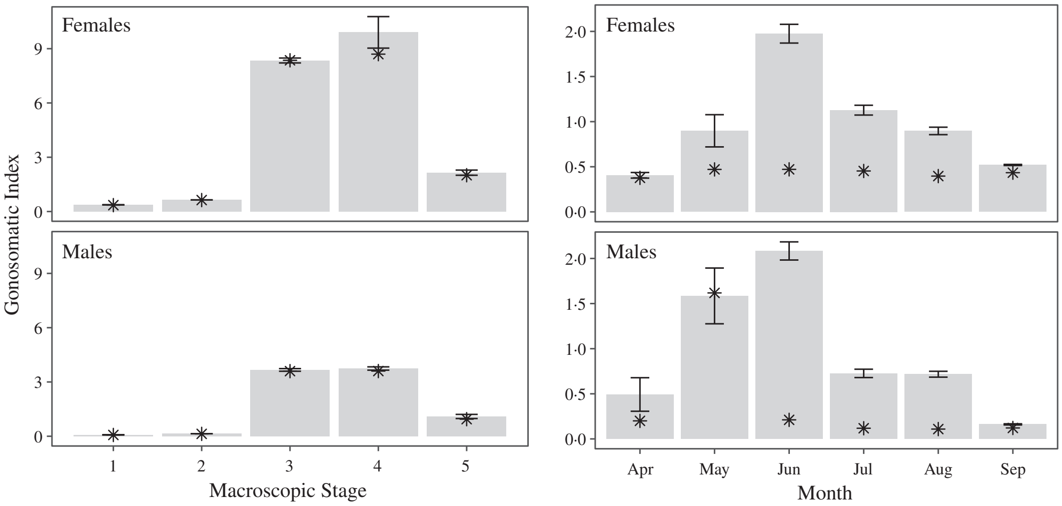

FIG. 2. Gonadosomatic index (I_G) distributions in each macroscopic gonad stage (left) and month (right; months with >3 observations only) for each sex. Bars = median I_G, error bars = standard error, asterisks = median I_G.

because no cases of misclassification involved fish that did not show histological indicators of sexual maturity.

The majority of males of macroscopic stages 1, 4 and 5 had the same microscopic stage (Table III), indicating that macroscopic staging of these stages was generally successful. In contrast, only 23% and 40% of macroscopic stage 2 and 3 fish, respectively, were assigned microscopic stage 2–3 combined. Ten fish of macroscopic stage 2 or 3 were found to have no cells beyond the spermatogonia stage and eight contained spermatozoa. The ambiguity in macroscopic and microscopic staging of males is probably associated with a continuum of spermatozoan development and turnover in males during the spawning season relative to the more discrete stages identifiable in females.

VARIATION IN GONADO-SOMATIC INDEX AND MACROSCOPIC STAGE

In both sexes, mean I_G was higher in stages 3 and 4 and to a lesser extent stage 5, compared with earlier developmental stages (Fig. 2). Gonad growth was greatest between April–June suggesting that June is the start of the spawning season for most individuals. Between July and September, mean I_G rapidly declined in both sexes, but there were a substantial number of outliers with high I_G throughout these months. The majority of the 12 932 I_G measurements were for fish captured in either 2011 (90·1%) or 2009 (7·0%), precluding a meaningful investigation of inter-annual variation in I_G. As an alternative indicator of overall spawning potential, visual inspection of mean macroscopic stage across years, for females of 500–1000-mm L_T sampled in June–July, did not reveal obvious inter-annual variations.

For fish sampled during the main spawning period, females and males showed a transition with increasing fish length from macroscopic stage 1 to stage 2, together with a small increase in I_G (Fig. 3). Females and males of macroscopic stages ≥3 showed a substantially larger I_G at lengths ≥800 mm for females and ≥600 for males. For females

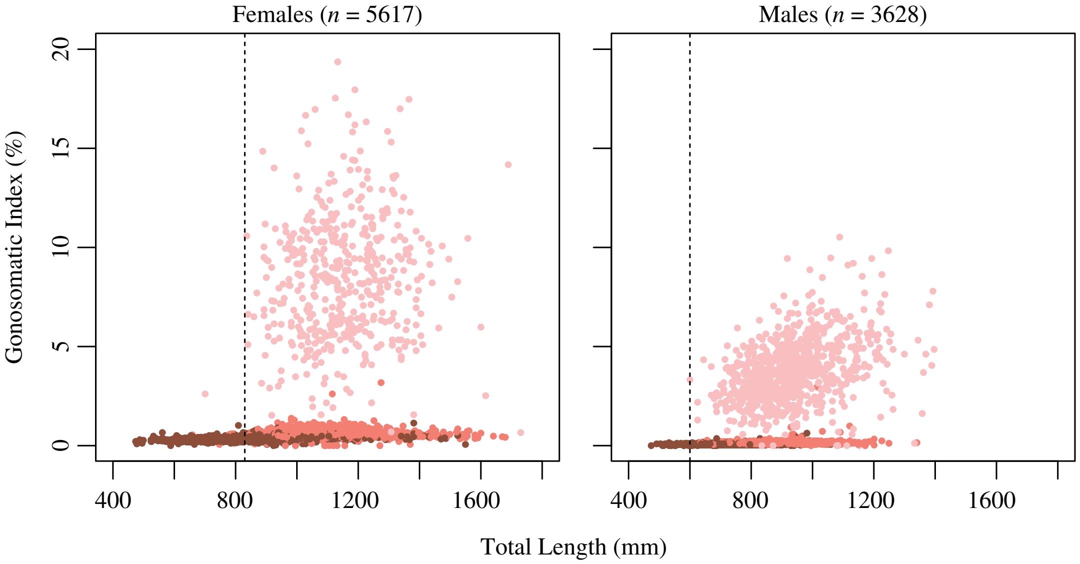

FIG. 3. Gonadosomatic index (I_G) by sex, stage and total length for *Dissostichus eleginoides* measured during the main spawning period (May–August). Dark red = stage 1, intermediate red = stage 2, light red = stages ≥3. Vertical dotted lines indicate the approximate size at first maturity, as indication by the minimum size at which fish transition to higher I_G values.

the length bins in which stage 2 and stages ≥3 were found largely overlapped. For example, some females at *c*. 1600 mm were still found to be at stage 2, indicating that females may rapidly revert to a resting appearance (as determined macroscopically) after spawning, or may not participate in spawning every season. This trend was slightly weaker for males, with most males >1100 mm being at stages ≥3, which may indicate that large males are able to maintain gonad stages ≥3 throughout the spawning season.

There was a positive trend between macroscopic gonad stage and fishing depth (Fig. 4). Stage 1 and 2 fish were encountered across the entire depth range fished. In

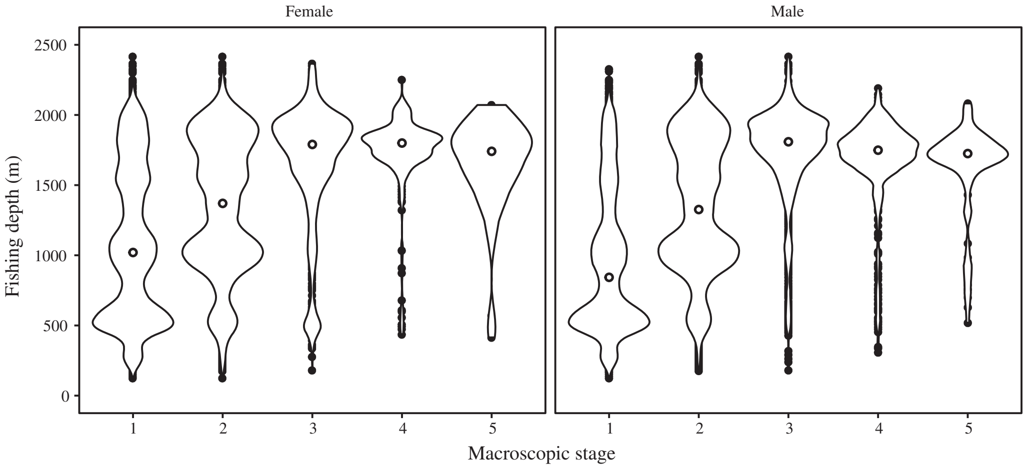

FIG. 4. Depth distributions of sex and gonad-stage groups for fish collected between May–August. Open circles = median fishing depth, filled circles = values outside of 1.5 times the 25% to 75% interquartile range.

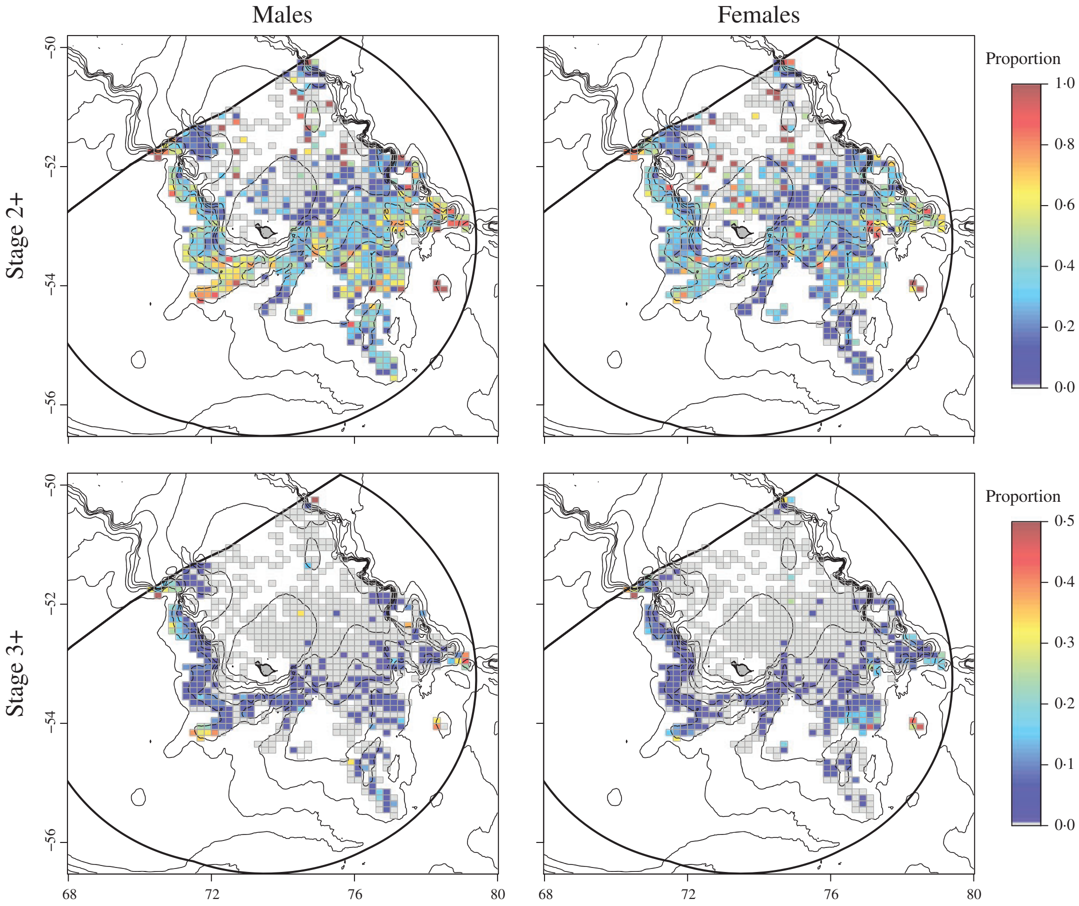

FIG. 5. Spatial variation in the proportion of *Dissostichus eleginoides* caught within the Australian EEZ (bold black line) around Heard Island and McDonald Islands that were macroscopic gonad stage 2+ (top panels) and stage 3+ (bottom panels) across all fishing gear types and years. Note the different legend scales for stage 2+ and stage 3+. Raster cells are of size 0.2° longitude and 0.1° latitude. Black lines = bathymetry contours (−400, −600, −1000, −1200, −1500, −2000, −3000 m; moving outward from Heard Island, shaded grey).

contrast, the majority of stage 3+ fish were encountered in depths of 1500–2000 m and small shifts in depth distributions towards shallower depths were observed between stages 3–5 (Fig. 4). The proportions of stage 2+ individuals were higher along much of the deeper slopes eastward, southward and westward of Heard Island, compared to shallower shelf areas to the north (Fig. 5). Stage 3+ fish of both sexes were more spatially constrained compared to stage 2+ fish, with occurrences primarily in the deepest areas close to the edge of the sampled area.

ESTIMATION OF AGE AT MATURITY

A total of 3594 female and 2556 male fish were aged and assessed for macroscopic maturity stage between 2004 and 2015 (Table IV). A_{50} estimates, obtained based on the assumption that fish of stages ≥2 were mature, were 13·9 and 14·1 years for females and males, respectively (Table S4 and Fig. S5, Supporting information).

The spatial distribution of fishing during years 2010–2015 was broader compared to years 2004–2009 (Fig. S6, Supporting information) and this spatial expansion

TABLE IV. Number of *Dissostichus eleginoides* assessed for macroscopic maturity stage and aged by sex and time period, for pooled and a sub-set of data. Estimated ages at 50% maturity (A_{50}) ± 95% C.I. (in parentheses) derived from 10 000 bootstrap samples

		All fishing gears and fishing depths pooled					Data subset: longline and depths of 600–1700 m				
		Number of fish					Number of fish				
Time period	Sex	Immature	Mature	Total	Proportion mature	A_{50} (95% C.I.)	Immature	Mature	Total	Proportion mature	A_{50} (95% C.I.)
2004–2015	Both	4318	1832	6150	0·30	13·9 (13·5–14·3)	–	–	–	–	–
	Female	2381	1213	3594	0·34	13·9 (13·5–14·3)	–	–	–	–	–
	Male	1937	619	2556	0·24	14·1 (13·3–15·0)	–	–	–	–	–
2004–2009	Both	2682	554	3236	0·17	15·8 (16·3–15·3)	729	420	1149	0·37	14·6 (14·0–15·3)
	Female	1418	381	1799	0·21	15·5 (16·1–14·9)	388	296	684	0·43	13·8 (13·2–14·6)
	Male	1264	173	1437	0·12	16·7 (18·0–15·6)	341	124	465	0·27	16·4 (15·1–18·2)
2010–2015	Both	1636	1278	2914	0·44	11·0 (11·4–10·5)	523	549	1072	0·51	12·9 (12·4–13·4)
	Female	963	832	1795	0·46	11·6 (12·2–11·0)	328	426	754	0·56	13·2 (12·6–13·8)
	Male	673	446	1119	0·40	9·9 (10·7–9·1)	195	123	318	0·39	12·0 (11·1–13·0)

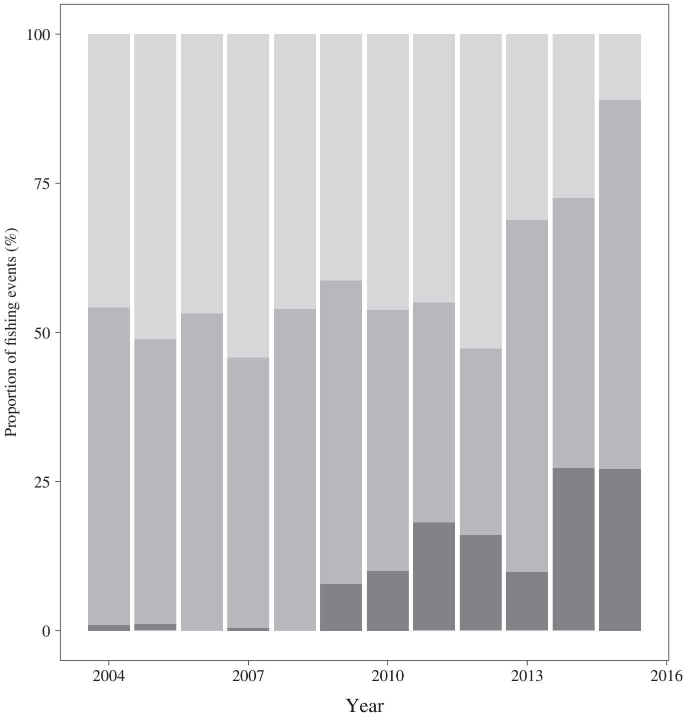

FIG. 6. Temporal changes in fishing-depth composition (both fishing gears pooled) between years 2004–2015. Light grey = <600 m, intermediate grey = 600–1700 m, dark grey = > 1700 m.

coincided with an increase in fishing depths (Fig. 6) along with increasing proportions of fishing events that used longline gear. To investigate the effect of these changes in fishery operation on A_{50} estimates, data were split into two time periods: 2004–2009 and 2010–2015. A total of 3236 and 2914 fish were aged and assessed for macroscopic maturity stage during 2004–2009 and 2010–2015, respectively (Table IV). Overall, only 17% of fish were mature between 2004 and 2009 compared with 44% between 2010 and 2015 (Table IV). Age-frequency histograms also indicated a broader female age distribution in the later period (Fig. 7).

Age-at-maturity ogives based on the assumption that stage 3+ fish were mature included only those individuals with clear macroscopic characteristics indicating that they were likely to spawn, or had recently spawned, in the season sampled. The resulting ogives gave unrealistically-high estimates of age at maturity (> 23 years) for all sex or time-period combinations however, with even the largest age classes for females never reaching 100% maturity (Fig. S7, Supporting information).

Age-at-maturity ogives based on the assumption that stage 2+ fish were mature accounted for stage 2 individuals that were mature, but resting when sampled. This was based on the observation that around 65% of stage 2 fish were likely to have already participated in spawning or had advanced to vitellogenesis and hence could be considered mature. Under this assumption, 100% maturity was reached for both sexes. A_{50} estimates were higher in 2004–2009 compared with 2010–2015, with a larger temporal change in A_{50} for females than for males (Fig. 7 and Table IV). Females achieved 50% maturity at 15·5 years during 2004–2009 and 11·6 years during 2010–2015; whereas males achieved 50% maturity at 16·7 years during 2004–2009 and 9·9 years during 2010–2015 (Fig. 7 and Table IV).

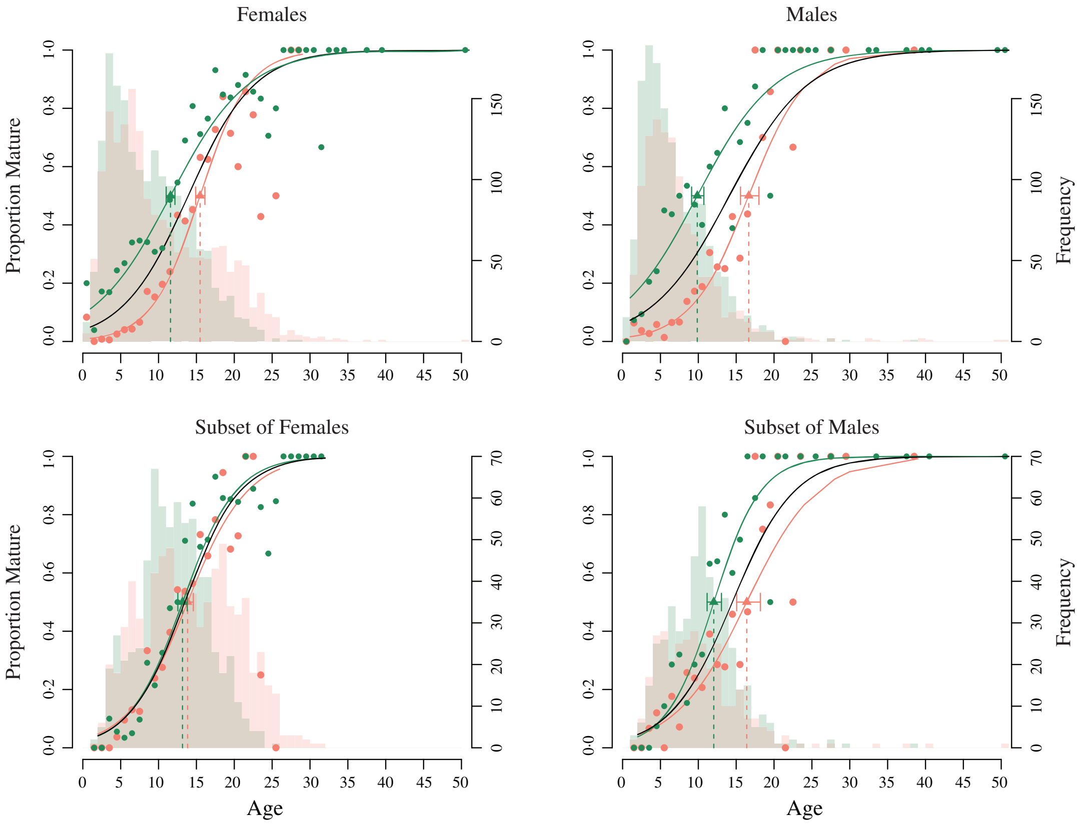

FIG. 7. Estimated age at maturity for female and male *Dissostichus eleginoides* for the periods 2004–2015 (black), 2004–2009 (●) and 2010–2015 (●), with fish of macroscopic gonad stage ≥2 considered to be mature. Top panels include data from all fishing gears and fishing depths pooled. Bottom panels include a subset of the data from longlines in fishing depths of 600–1700 m. Points are proportions of fish that were mature (in 1-year age bins), solid curves are fitted values obtained by logistic regression, triangles and dashed lines indicate age at 50% maturity (A_{50}), error bars indicate 95% confidence intervals for A_{50} obtained using nonparametric bootstraps and the percentile method, bars are age-frequency histograms for both time periods.

The use of stage 2+ as the criteria for sexual maturity may underestimate age at maturity in the population to some degree because some stage 2 fish lacked indicators of having spawned in the past. Assuming that the progression from cortical alveoli stage to hydration in notothenioid fishes can take up to 2 years (Kock & Kellermann, 1991), an offset of 2 years was added to all stage 2 fish and age-at-maturity parameters were re-estimated with this offset. The influence of the offset was small and the estimated maturity parameters were similar, with female $A_{50} = 14{\cdot}2$ years (95% C.I. = 13·8–14·5; 10 000 bootstrap replicates), male $A_{50} = 12{\cdot}8$ years (95% C.I. = 12·3–13·3; 10 000 bootstrap replicates) and sexes-pooled $A_{50} = 13{\cdot}7$ years (95% C.I. = 13·4–14·0; 10 000 bootstrap replicates).

Maturity ogives were also fitted to longline-captured fish from fishing depths between 600 and 1700 m (Fig. 7). These depths were similarly represented during both time periods in data from longlines. When comparisons of A_{50} estimates between time periods were limited to the same gear type and similar fishing depths, the change in A_{50} between 2004–2009 and 2010–2015 was smaller, particularly for females (0·6 years; Fig. 7 and Table IV), compared with estimates made using all gears and depths pooled

(3·9 years). For males, A_{50} decreased by 4·4 years between periods 2004–2009 and 2010–2015 using the longline data from depths of 600–1700 m, compared to 6·8 years using data from all gears and depths (Table IV).

DISCUSSION

Consistent biological sampling by observers since the HIMI fishery commenced, and the targeted sampling during the 2011 spawning season, enabled detailed investigation of spatial and temporal patterns of *D. eleginoides* reproductive biology. The spawning season is similar to that reported in other studies, with a review by Collins *et al.* (2010) noting that the spawning seasons reported for *D. eleginoides* throughout its range are generally between April and August. This timing may have evolved so that larvae are likely to emerge coincident with the spring-time increase in productivity (Dragon *et al.*, 2011).

The deep slopes along the western margin of the Kerguelen Plateau, in both the French and Australian EEZs, are likely to be used as spawning habitat by *D. eleginoides* (Mori *et al.*, 2016). Although the productive shallow plateau waters at HIMI may provide attractive foraging opportunities for larger fish (Améziane *et al.*, 2011; Welsford *et al.*, 2011; Park *et al.*, 2014), spawning in deeper slope environments may provide greater benefits *via* reduced predation pressure from elephant seals *Mirounga leonina* and sperm whales *Physeter microcephalus*, which generally forage in depths of <1000 m (Watwood *et al.*, 2006; McIntyre *et al.*, 2011). Furthermore, recent hydrodynamic modelling revealed that spawning on deep western slopes at HIMI could enhance the retention of eggs and larvae over the shallow Plateau, thereby enhancing offspring fitness and survival (Mori *et al.*, 2016; Péron *et al.*, 2016). There is evidence in this study that important spawning habitats may extend further south into the Australian EEZ than previously thought and that they may also occur on the slopes south of HIMI. Hydrodynamic models for the area indicate a retroflexion of the northern and southern filaments of the Polar Front along the eastern margin of the Kerguelen Plateau (Park *et al.*, 2008; van Wijk *et al.*, 2010), which may be a feature that transports eggs and larvae from these upstream locations in the south-west to near the shallow north-eastern end of the Kerguelen Plateau where the smallest juveniles have been recorded (Duhamel & Hautecoeur, 2009; Mori *et al.*, 2016).

Sexual dimorphism in I_G and maturation has also been reported for both *Dissostichus* species in other locations and is most likely influenced by lower energetic cost and smaller abdominal space required to produce sperm compared with eggs (Lord *et al.*, 2006; Arana, 2009). The sizes at first maturity for males (*c.* 600 mm) and females (*c.* 800 mm), as indicated by the L_T at which I_G transitioned to higher values, were higher than in other studies. For example, Lord *et al.* (2006) reported that male and female *D. eleginoides* attained macroscopic stages ≥3 at *c.* 500 and 540 mm, respectively, at the Kerguelen Islands during 2002–2003. It is possible that there are genuine differences between these populations. Differences in size at first maturity of females may also be influenced by interannual variability in the portion of the population that participates in spawning in any 1 year.

A lower overall spawning fraction in a particular year may be the result of variation in the spawning activity of particular size classes. For example Everson & Murray (1999) showed that at South Georgia >30% of the size classes of fish that were mature and in spawning condition in 1996 did not spawn in 1997. The majority of samples of I_G in this study derived from a single season and evidence from histological analysis estimated that some stage 2 fish may have been resting after spawning in the past, suggesting that 2011 at HIMI may have been analogous to 1997 at South Georgia. In light of this, comparisons between macroscopic staging and histological assessment in 2011 may not be applicable across all years. Histological analysis of samples collected over several years, collected both prior to, during and after the spawning season would allow a better characterization of interannual variability in spawning fraction and analysis of rates of vitellogenesis and POF breakdown. Such data would also allow the exploration of relationships between spawning fraction, environmental conditions and subsequent recruitment; and investigations into interannual variation in methods of assigning macroscopic stage.

The occurrence of large females with I_G values indistinguishable from smaller immature fish suggested that females may rapidly revert to a resting stage after spawning, or may not participate in spawning every season. In a given season, non-spawning mature females may either fail to commence vitellogenesis, or resorb oocytes entering into vitellogenesis (Rideout *et al.*, 2005). The energy saved by not spawning in a given year may lead to increased survival or spawning success in subsequent years (Rideout *et al.*, 2005; Rideout & Tomkiewicz, 2011). In this context, the energetic cost of provisioning large yolky eggs (Evseenko *et al.*, 1995) may explain why a portion of mature female *D. eleginoides* do not spawn in a given season at HIMI. The occurrence of non-spawning mature fish is an important consideration in recruitment models because it may lead to an overestimation of the true number of spawners and expected recruitment (Rideout *et al.*, 2005).

Previous studies estimating size at maturity for *D. eleginoides* have used stage 3 as the threshold for estimating the proportion of the population that is mature [*e.g.* southern Chile (Arana, 2009), South Georgia (Everson & Murray, 1999) and the Kerguelen Islands (Lord *et al.*, 2006)]. In this study, the occurrence of mature resting fish that were macroscopically indistinguishable from first-maturing fish led to age-at-maturity estimates on the basis of stage 3+ fish being mature to be higher than those reported elsewhere (Collins *et al.*, 2010), an issue also identified by Everson & Murray (1999). Under the assumption that *D. eleginoides* reach maturity at gonad stage 3, the exclusion of stage 2, albeit mature and resting, *D. eleginoides* from the proportion considered to be mature resulted in unrealistically high estimates of age at maturity. Estimates of age at maturity using stage 2 as the threshold produced results that were generally consistent with other stocks (Collins *et al.*, 2010). They were also likely, however, to be biased towards younger–smaller values as not all stage 2 fish had microscopic characteristics indicating they were likely to be mature in the season they were sampled. Comparison with A_{50} estimates calculated with an offset of 2+ years to the ages of stage-2 fish suggested that this bias is likely to be small.

The observed temporal changes in age at maturity may be the result of sampling bias brought about by historical variation in the operation of the HIMI fishery. In particular, this study highlighted a spatial expansion of fishing into deeper slope habitats and an increasing prevalence of longline fishing. Fishing at these depths sampled a greater proportion of larger and older fish with higher I_G and more advanced maturity stages. In other studies, spatial variation in maturity responses have been attributed to local opportunities for growth and possibly also survival (Williams *et al.*, 2003*a*; Olsen & Vøllestad, 2005). Hence a shift in sampling towards deeper habitats potentially occupied by earlier-maturing fish could contribute to the temporal shift in age at maturity reported here. The issue of spatial and temporal segregation of mature spawning fish away from the juvenile (Péron *et al.*, 2016) and resting population and the potential for sampling biases influencing estimates of size at maturity, has been also noted *D. mawsoni* (Parker & Grimes, 2010).

The outcomes of attempts to account for sampling biases in each time period in this study varied between sexes and therefore it is important to consider other factors that may have influenced temporal variations in maturation. Water temperature can influence the development and maturation of teleosts, either directly or *via* changes in metabolism, growth or condition (Hutchings & Jones, 1998; Cardinale & Modin, 1999; Gerritsen *et al.*, 2003; Domínguez-Petit *et al.*, 2008). For example, smaller sizes at maturity for male and female sockeye salmon *Oncorhynchus nerka* (Walbaum 1792) have been reported in years when sea surface temperatures were relatively warm (Cox & Hinch, 1997). This change may have been caused directly by increased metabolic demand, or indirectly by oceanic changes that influence food acquisition (Cox & Hinch, 1997). Between years 1992 and 2007, the northern branch of the Polar Front shifted nearly 10° latitude, from the northern to the southern end of the Kerguelen Plateau (Sokolov & Rintoul, 2009). The Polar Front is associated with meridional gradients of temperature, salinity, nutrients and plankton communities (Sokolov & Rintoul, 2009). Therefore the southward shift of the front is hypothesized to drive warming and ecosystem changes (Sokolov & Rintoul, 2009) and these changes could influence maturation of *D. eleginoides* on the Kerguelen Plateau.

Altered mortality schedules brought about by fishing can also lead to changes in population dynamics and life-history traits (Stearns, 1992; Domínguez-Petit *et al.*, 2008; Sharpe & Hendry, 2009; Li *et al.*, 2011). Reductions in population size as a result of fishing may reduce intraspecific competition for space and resources; thereby promoting accelerated growth and earlier maturation (Heino & Godø, 2002) and influencing natural mortality (Sharpe & Hendry, 2009). Furthermore, life-history theory predicts that fishing mortality can favour genetic evolution towards earlier sexual maturation at smaller body sizes (Jørgensen *et al.*, 2007; Sharpe & Hendry, 2009), especially if fishing is non-uniformly selective across body sizes, maturity stages, behaviours or morphologies (Heino & Godø, 2002; Jørgensen *et al.*, 2007). Probabilistic maturation reaction norms (PMRNs) are functions that describe the probability that an immature individual of a given age and size will mature during a specified time interval (Heino *et al.*, 2002; Dieckman & Heino, 2007; Sharpe & Hendry, 2009). Although this method is increasingly used in empirical studies in conjunction with age at maturity, it was not possible to generate PMRNs in the present study because this method requires separating plastic and genetic effects on maturation (Sharpe & Hendry, 2009). In this study, the aggregation of data into time periods, which coincided with variation in sampling regime, precluded empirical investigations of the effects of altered mortality schedules on maturation and this highlights the importance of the ongoing programme of scientific observation in the HIMI fishery.

This study was unable to directly investigate the effects of environmental change or fishing pressure on the maturation of *D. eleginoides* at HIMI, but the variability in age at maturity between gear types and across depths, suggests that changes in sampling bias through time were important drivers of changes in maturity estimates. These biases, along with the uncertainty associated with the selection of either stage 2+ or stage 3+ as the criteria for maturity, prompted the generation of multiple candidate estimates of

A_{50} to be used in stock assessment models. In consideration of the hypothesized sources of bias, it is suggested that *D. eleginoides* stock assessments include age-at-maturity estimates based on longline and trawl data from years ≥2004 (*i.e.* all years pooled) and considering stages ≥2 as mature. Furthermore, estimates for both sexes pooled will need to be used in stock assessment models that cannot incorporate differences in maturation rates between males and females.

Using spatio-temporal dynamics in maturation of *D. eleginoides* as an example, this study highlighted the importance of considering the influence of fishery operations when estimating life-history traits. In particular, life-history traits may appear to be variable if there is spatial structuring of these traits within the population and if sampling is not consistent in time and space. Furthermore, identification of the occurrence of mature resting females was facilitated by the integration of I_G data with macroscopic and microscopic gonad-staging methods; this approach can assist in the interpretation of macroscopic gonad stages in other teleosts.

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Supporting Information

Supporting Information may be found in the online version of this paper:

FIG. S1. (a) Proportion by 20 mm total length (L_T) classes of *Dissostichus eleginoides*: ——, trawl data; ——, longline data; - - - -, both fishing gears. (b) Sex composition by 100 mm L_T classes of *D. eleginoides* for which total length and sex data were available. ■, females; ■, male; ■, unknown sex; - - -, 1:1 sex ratio.

FIG. S2. Appearance of oocytes developmental stages in *Dissostichus eleginoides* ovaries stained with haemotoxylin and eosin: (a) early perinucleus (b) late perinucleus, (c) cortical alveoli, (d) earlyvitellogenesis, (e) mid vitellogenesis, (f) late vitellogenesis, (g) early migratory nucleus, (h) late migratory nucleus, (i) post migratory nucleus, (j) hydrated–mature oocyte.

FIG. S3. Appearance of (a) recent and (b) old post-ovulatory follicles, (c) oocytes undergoing atresia and (d) an ambiguous tissue structure with intermediate characteristics of both POFs and atretic oocytes.

FIG. S4. Appearance of developmental stages in *Dissostichus eleginoides* testes stained with haemotoxylin and eosin: (a) immature, (b) developing, (c) spawning, (d) spent.

FIG. S5. Estimated age at maturity for females and males sampled between years 2004–2015. Fish of macroscopic gonad stage ≥ 2 were considered to be mature. Points are proportions of fish that were mature pooled in 1-year age bins, solid curves are fitted values obtained by logistic regression, triangles and dashed lines indicate age at 50% maturity (A_{50}) with error bars indicating 95% confidence intervals for A_{50} obtained using nonparametric bootstraps and the percentile method. Grey bars are age-frequency histograms.

Fig. S6. Spatial extent of fishing during years (a) 2004–2009 and (b) 2010–2015 within the Australian EEZ (——) around Heard Island and McDonald Islands. ■, Areas where ≥ one fishing event occurred in the given time period. Raster cells are of size 0·2° longitude and 0·1° latitude. ——, Isobaths: 400, 600, 1000, 1200, 1500, 2000, 3000 m depth.

Fig. S7. Estimated age at maturity for females and male *Dissostichus eleginoides* for the periods 2004–2009 (●) and 2010–2015 (●), with fish of macroscopic gonad stage ≥ 3 considered to be mature. Points are proportions of fish that were mature pooled in 1-year age bins, solid curves are fitted values obtained by logistic regression, triangles and dashed lines indicate age at 50% maturity (A_{50}), orange and green error bars indicate 95% confidence intervals for A_{50} obtained using nonparametric bootstraps and the percentile method, orange and green bars are age-frequency histograms for both time periods.

Table S1. Numbers of *Dissostichus eleginoides* for which length and mass data were collected. The number of *D. eleginoides* with sex, gonad stage and gonad weight data are provided in parentheses. Year 2011 included a winter longline voyage with a particular focus on the collection of gonad stages and samples (highlighted in bold).

Table S2. Description of oocyte development in *Dissostichus* spp. and its corresponding macroscopic (Kock & Kellermann, 1991; Table I) and microscopic [based on descriptions in West (1990), Ewing & Lyle (2009) and Murua *et al.,* (2003)] developmental stages.

Table S3. Characteristics of post-ovulatory follicles (POFs) and atretic structures identified in *Dissostichus eleginoides* ovaries (based on descriptions in West [1990], Ewing & Lyle [2009] and Murua *et al.* [2003]).

Table S4. Description of spermatozoan development in *Dissostichus* spp. and corresponding macroscopic (Kock & Kellermann, 1991) and microscopic developmental stages.

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