Spawning area and season of butterfly kingfish (*Gasterochisma melampus*), a large scombrid adapted to cooler temperate southern water

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Abstract. In the present study we investigated spawning of the butterfly kingfish (*Gasterochisma melampus*), a Scombridae species distributed in circumpolar temperate waters of the Southern Hemisphere in the Atlantic, Indian and Pacific oceans. Using data from 25 564 individuals collected by longline operations from 1987 to 1996, analysis of the gonadosomatic index, maturity based on oocyte size and the presence of hydrated eggs revealed that the spawning area was between longitude 85 and 130°W and latitude 28 and 41°S in the south-east Pacific Ocean, and that the spawning season was from mid-April to mid-July. Length–frequency data suggested that larger fish arrived and spawned earlier, whereas smaller fish did so later. The species has distinctive reproductive characteristics compared with other Scombridae: it produces large hydrated eggs 1.6 mm in diameter, sea surface temperatures in the spawning area were as low as 14–18°C and more than 80% of fish were female. The south-east Pacific Ocean may be the only (and is at least the major) spawning area of the species. Butterfly kingfish is a single stock that migrates to the Atlantic, Indian and Pacific oceans to feed and returns to the south-east Pacific Ocean to spawn.

Introduction

There have been few studies of the ecosystems in the circumpolar temperate waters of the Southern Hemisphere at latitudes between 30 and 50°S extending across the Atlantic, Indian and Pacific oceans (Itoh and Sakai 2016). Representative large pelagic fish species distributed in this area are the southern bluefin tuna (*Thunnus maccoyii*), albacore (*Thunnus alalunga*), butterfly kingfish (*Gasterochisma melampus*), slender tuna (*Allothunnus fallai*), opah (*Lampris guttatus*), blue shark (*Prionace glauca*) and the porbeagle (*Lamna nasus*). Although commercially important species such as tunas have been studied well (e.g. Caton 1994; Murray 1994), there have been few studies of other species, such as the butterfly kingfish (but see Semba *et al.* (2013) for the porbeagle).

The butterfly kingfish is a large Scombridae species that reaches a fork length (FL) of 190 cm; the genus *Gasterochisma* has only this single species. The fish's silver body is covered with large cycloid scales and has many distinctive morphological characteristics that differentiate it from other Scombridae (Collette *et al.* 2001). The general distribution of the species was reported by Warashina and Hisada (1972) and its sporadic occurrence off Argentina, Brazil and Hawaii has been reported (Ito *et al.* 1994;

Rotundo *et al.* 2015). The fish's physiology is interesting in that it has a brain heater (Carey 1982). The taxonomic position of the species, in terms of the evolution of endothermy, has been somewhat controversial (Block *et al.* 1993; Collette *et al.* 2001). There is a consensus that the species belongs to the Scombridae; however, studies based on morphology have hypothesised that it belongs to the independent subfamily Gasterochismatinae (Kohno 1984; Ito *et al.* 1994; Collette *et al.* 2001), whereas studies in molecular biology have hypothesised that it belongs to the subfamily Scombrinae, with tunas and mackerels (Block *et al.* 1993; Ito *et al.* 1994; Collette *et al.* 2001; Qiu *et al.* 2014).

In commercial tuna longline fishing, the butterfly kingfish has been a bycatch of southern bluefin tuna fishing by the Japanese fleet since the 1970s and is retained in the vessels for market, although the price received is not particularly high (Warashina and Hisada 1972). Because it appeared that the butterfly kingfish was distributed at high densities in the south-east Pacific Ocean, which is not a fishing ground for southern bluefin tuna, a research project was run for 10 years from 1987 by the Japan Marine Fishery Resources Research Center (JAMARC; now the Marine Fisheries Research and Development Center of the Fisheries and Education Research Agency) to

Table 1.   Summary of information on research cruises for butterfly kingfish

Cruise number	Date of longline operation		Number of operations		Area of longline operation	Assumed area for fish	Number of butterfly kingfish caught
	Start	End	All	With butterfly kingfish			
1	28 Oct. 1987	23 Mar. 1988	101	98	81–170°W, 22–53°S	Feeding	2590
2	8 Apr. 1988	27 Sep. 1988	104	95	85–144°W, 28–49°S	Spawning	1026
3	21 Oct. 1989	20 Mar. 1990	94	80	86–117°W, 31–48°S	Feeding	3577
4	12 Apr. 1990	13 Sep. 1990	103	78	85–120°W, 22–47°S	Spawning	1902
5	31 Oct. 1991	24 Mar. 1992	85	84	83–117°W, 35–50°S	Feeding	3641
6	8 Apr. 1992	28 Aug. 1992	99	95	88–121°W, 31–44°S	Spawning	2508
7	9 Oct. 1993	20 Mar. 1994	115	107	96–170°W, 30–56°S	Feeding	3238
8	14 Apr. 1994	15 Sep. 1994	120	112	81–115°W, 28–47°S	Spawning	3593
9	12 Nov. 1995	31 Mar. 1996	86	57	76–116°W, 30–60°S	Feeding	1464
10	1 Apr. 1996	19 July 1996	84	69	87–102°W, 29–35°S	Spawning	2025
Total			991	875			25 564

explore the fishing grounds where butterfly kingfish could become the main target species. During these research cruises, the spawning area was located through an analysis of captured fish with ripe ovaries. The results have not been published before in an international peer-reviewed scientific journal, although they have been reported in domestic documents (e.g. Anonymous 1997). Herein we reanalyse the data, report on the spawning season, area and fish size and discuss the characteristic spawning ecology of this species.

Materials and methods

There were 10 longline research cruises from 1987 to 1996 (Table 1). One vessel, which was usually used for commercial tuna longline fishing, was chartered for each cruise and longline operations were conducted in the same way as for commercial operations. In the usual pattern, a total of 2400 hooks was used for each operation, and between 10 and 15 branch lines were used between two floats that set the hooks at depths of 80–220 m; this depth range was based on calculations of the catenary curve of the longline (Yoshihara 1951). Five of the ten cruises aimed to catch spawning fish. All applicable international, national and institutional guidelines for the care and use of animals were followed.

When an individual butterfly kingfish was caught, its FL (cm) and weight (kg) were measured and its sex identified by gonad examination. Both ovaries were weighed and their weights summed (in tens of grams) and maturation was classified into the following five stages by macroscopic visual observation of the fish while still on board: (1) immature, with no oocytes; (2) most advanced oocytes 0.2–0.3 mm in diameter; (3) most advanced oocytes 0.4–0.5 mm in diameter; (4) most advanced oocytes 0.8–1.1 mm in diameter or larger, translucent and easy to separate from the surrounding tissue, the ovaries are enlarged and the ovarian membrane thin and fragile; and (5) ovaries larger than Maturity Stage 1 but smaller than Maturity Stage 4, with an increased size of the ovarian cavity.

The presence of hydrated eggs was recorded arbitrarily. Seventeen females were found that had hydrated eggs in their ovaries; this is classified as Maturity Stage 4 and is strong evidence of spawning having taken place. Samples were cut

from one ovary from five of these fish and preserved in 5% formalin in seawater on-board. Later, in the laboratory, the diameter of 100 randomly selected hydrated eggs from each sample was measured at a resolution of 0.1 mm using a micrometer under a dissecting microscope.

In the present data analysis, the gonadosomatic index (GSI) was used as the criterion of maturation rather than the afore-mentioned maturation stages used in on-board gonad observations because the on-board researchers differed from cruise to cruise and the classifications they made may have been inconsistent. The GSI was calculated as follows:

$$GSI = (gonad\,weight) \div (body\,weight - gonad\,weight) \times 100$$

Judgment of maturity solely on the basis of the GSI is problematic in that the GSI cannot distinguish a spent ovary from an immature ovary; however, the GSI is effective if data on the size of the most advanced oocyte, or histological observations, are also used (Schaefer 2001). We attempted to evaluate maturity by approximating the relationship between GSI and the proportion of females in Maturity Stage 4 using a logistic model and a binomial distribution based on the dataset from 1994, the year in which the largest dataset was obtained. The GSI at which 80% of fish in Maturity Stage 4 met the criteria for maturity was used, with GSIs at which 20 and 50% of fish in Maturity Stage 4 met the criteria were used for comparison.

The spatial and temporal occurrences of mature fish were examined on the basis of the GSI by aggregating the data by 1° of latitude and 5° of longitude, or by month divided into one-third intervals (i.e. Days 1–10, Days 11–20 and Day 21 to the end of the month); the spawning area and season were then estimated accordingly. Furthermore, we analysed the relationship between length–frequency and the proportion of mature fish in the spawning area, compared the water temperatures (sea surface temperature at noon during the longline operation) inside and outside the spawning area, mapped the distribution of monthly catch per unit effort (CPUE; the number of butterfly kingfish caught by 1000 hooks) and examined the sex ratio by size. Analyses were performed using R, ver. 3.2.3 (R Foundation for Statistical Computing, Vienna, Austria).
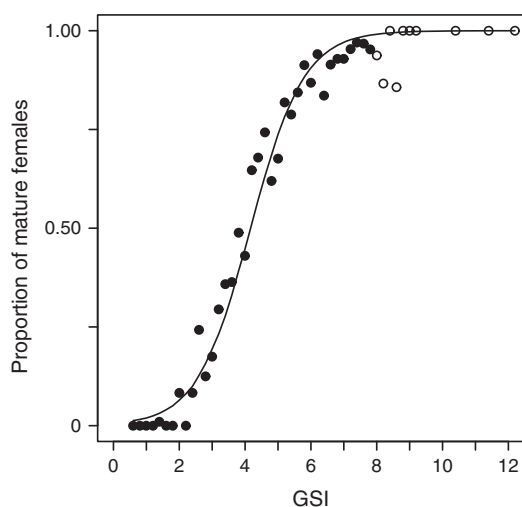
Fig. 1. Proportion of mature females as determined by the gonadosomatic index (GSI) of butterfly kingfish. Symbols are observed data of the proportion of mature females (in GSI bins of 0.2). Solid and open circles represent >20 females and ≤20 females respectively. The solid line is the estimated logistic curve. The total number of fish was 2996.

Results

The parameter values for the logistic model that approximated the proportion of mature females (Maturity Stage 4) from the GSI were estimated as follows (Fig. 1):

$$\text{Proportion of mature females} = 1 / \left(1 + e^{-1.236 \times GSI + 5.151}\right)$$

In the model, 80, 50 and 20% of females were mature at GSI = 5.3, 4.2 and 3.0 respectively. In the following description, GSI >5 is used as the maturity criterion; data for females with GSI >3 and >4 are presented in the figures for comparison.

The spatial range of the butterfly kingfish caught extended from 76 to 169°W and from 28 to 54°S. Mature females (GSI >5) occurred in the northern part of this range, from 85 to 130°W and from 28 to 41°S (Fig. 2). Mature females were found from mid-April to mid-July and most frequently in mid-May (Fig. 3). This range was validated by the occurrence of ovaries containing hydrated eggs (see numbers in Fig. 3).

The smallest mature female with GSI >5 had a FL of 103 cm. In the mature group, substantial numbers of females were found with FL >120 cm (Fig. 4). It would not have been appropriate to estimate the length at which 50% of the population reached maturity (Schaefer 2001) from our data, because we did not know the number of females distributed in the spawning ground as a proportion of the total population. In our analysis of length–frequency according to one-third month intervals, larger fish were abundant in mid-April, when the mode of the FL was 165 cm; the fish then became smaller as the month progressed, reaching a FL mode of 135 cm in mid-June. The proportion of mature females was high in all size classes in the early period, from mid-April to late May; among larger fish (>150 cm FL) this proportion decreased from early June onward. Therefore, these observations may indicate that larger fish arrived and
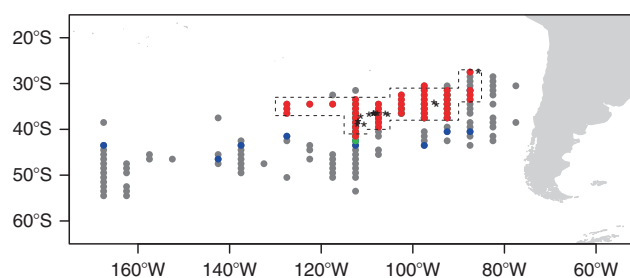

Fig. 2. Occurrence of mature female butterfly kingfish, by 1° latitude and 5° longitude squares. Red, green, and blue represent the occurrence of at least four fish with a gonadosomatic index of more than 5, 4 and 3 respectively. Grey dots represent catches of at least two fish. Asterisks are the locations of the start of longline operations in which females with hydrated eggs were caught. The total number of fish was 15 413. The polygon shows the defined spawning area used for further analysis.
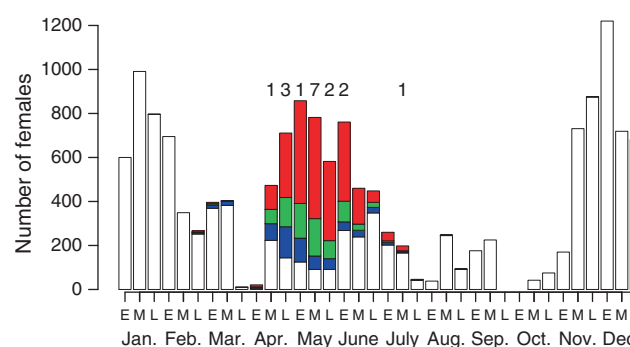

Fig. 3. Numbers of female butterfly kingfish by maturity per 10-day period. E, the first 10 days of each month; M, the second 10 days of each month; L, late in the month (from Day 21 until the end of the month). Red, green and blue denote gonadosomatic indices (GSIs) >5, 4–5 and 3–4 respectively. White bars denote GSIs <3. Numbers above the bars are the number of females with hydrated eggs. The total number of fish was 15 413.

spawned early in the spawning season, whereas smaller fish spawned later in the season. However, the larger fish seemed to stay in the spawning area after spawning.

The temperature of the water where mature fish were found (as inferred from the sea surface temperatures during longline operations) was frequently in the range 14–18°C, whereas the temperature outside the spawning area was lower (Fig. 5). The suitability of this temperature range for spawning was further supported by the presence of fish with ovaries containing hydrated eggs (see numbers in Fig. 5).

Sex was skewed towards female (85.3% in the spawning area and 77.1% outside the spawning area; Fig. 6). The percentage of females in the spawning area was ~50% up to 125 cm FL; it then increased linearly and reached almost 100% at 160 cm FL. The percentage of large males (e.g. 140 cm FL) was larger outside than inside the spawning area.

Examination of the monthly CPUE distribution showed that the area in which fish were caught moved to the spawning area from the south in April and were widely distributed in the spawning area in May, which may indicate fish movement (Fig. 7). The area in which fish were caught was concentrated
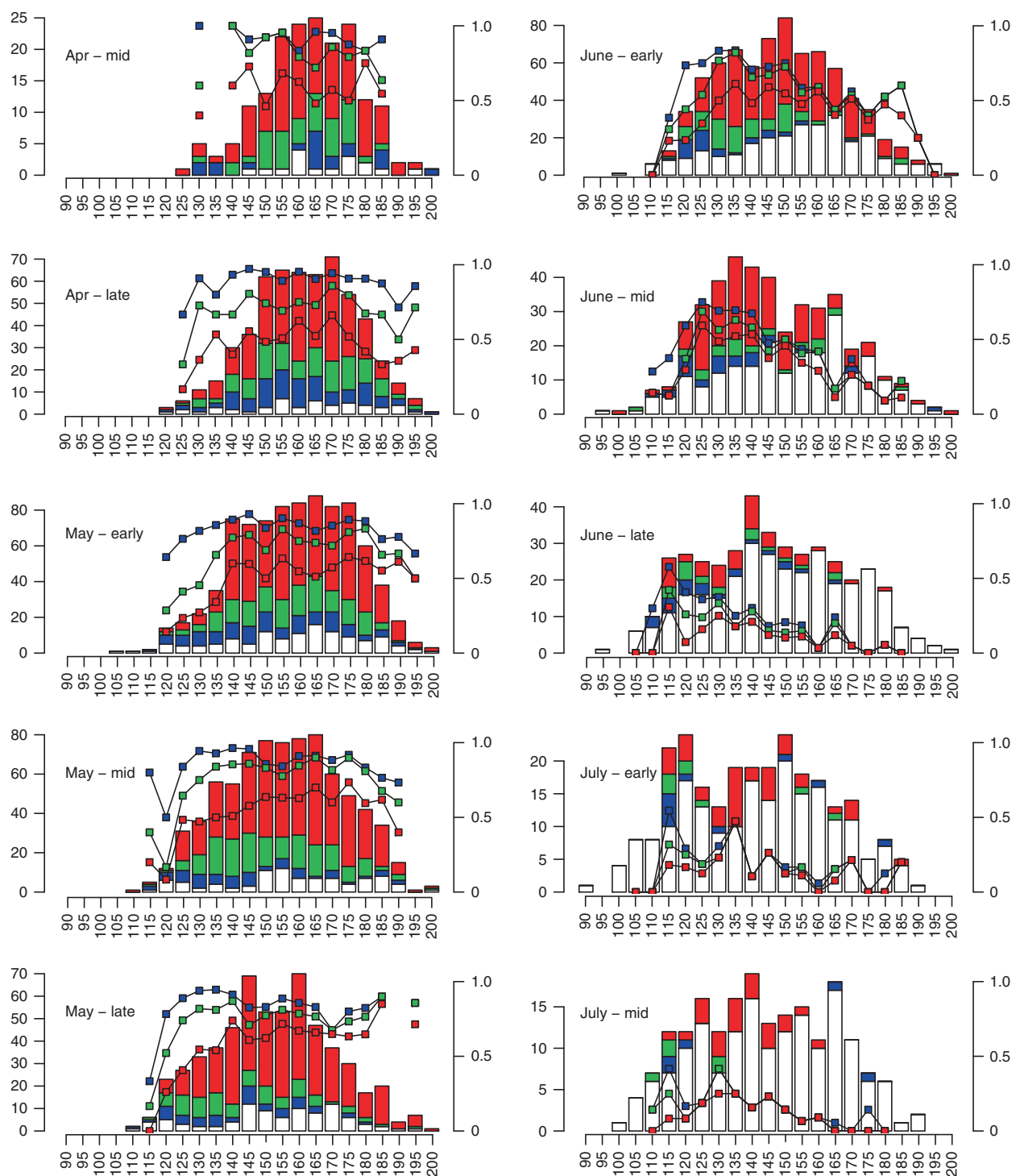
Fig. 4. Numbers of female butterfly kingfish by maturity stage and fork length (in 5-cm bins) presented for one-third monthly intervals (early, Days 1–10; mid, Days 11–20; late, Day 21 to the end of the month). Red, green and blue columns denote gonadosomatic indices (GSIs) >5, 4–5 and 3–4 respectively. White columns denote GSIs <3. Lines show the proportion of mature fish (right-hand *y*-axis). Points on the lines representing at least five fish are shown. Fork length (cm), number of females, and proportion of mature fish are indicated by the *x*-axis, left y-axis, and right y-axis respectively.

in the eastern half of the spawning area in June and July, but note that longline operations were not conducted in the western half of the area in these months. Fish were still being caught in the spawning area in August and September. The distribution of mature females was similar to that of the CPUE. Hydrated eggs were spherical, with individual mean diameters ranging from 1.55 to 1.74 mm; the mean diameter of eggs from five individuals was 1.64 mm (Table 2).
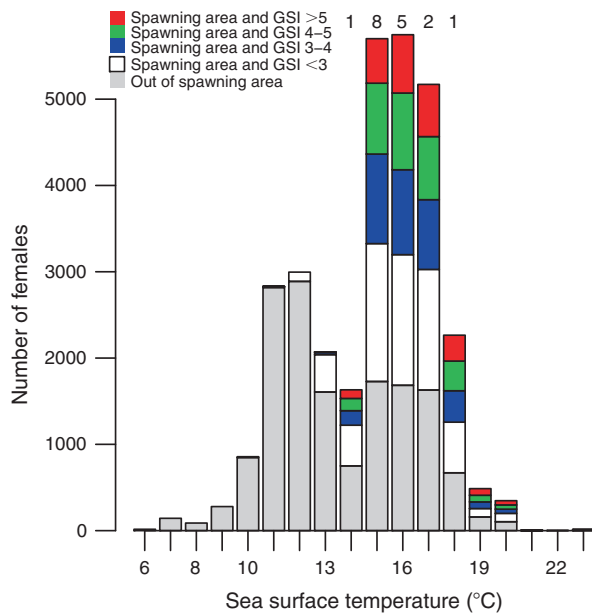
Fig. 5. Number of female butterfly kingfish caught according to sea surface temperature. Numbers above the columns are the number of females with hydrated eggs. The total number of fish was 15 413.
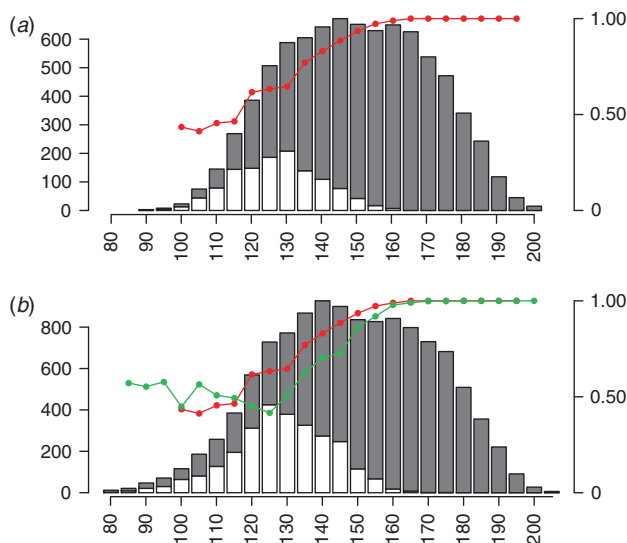

Fig. 6. Length frequencies of butterfly kingfish by sex (*a*) inside and (*b*) outside the spawning area. Open columns show the number of males; shaded columns show the number of females. Red and green lines show the proportion of females (right-hand *y*-axis), as shown for at least 21 fish per data point. The red line in the (*b*) is the same as that shown in (*a*).

Discussion

From our data, we determined the previously unknown spawning season and area of butterfly kingfish. The dataset contained information on a large number of fish sampled over 10 years, throughout most of the year, from an extensive area of the south-eastern Pacific Ocean. In some months there were areas where no surveys were conducted. However, because the survey covered 10 years and actively targeted butterfly kingfish, we consider it is

highly unlikely that butterfly kingfish would have been distributed at high temporal and spatial densities in areas of the southeastern Pacific Ocean missed by the survey.

It is possible that the spawning area and season were wider than those shown in the present study, and it is possible that they varied annually with the environmental conditions, stock status or both. Logbook data of Japanese longline fishery contain details of the butterfly kingfish catch since 1994. The data showed that, from June to August, there were some butterfly kingfish catches at additional times and in additional locations as bycatch of fishing targeting other tuna species in the area east to north-east of our delineated spawning area, although these catches were small in number and low in CPUE. Note that commercial fishing targeting butterfly kingfish in the southeastern Pacific Ocean has not been developed further since these data were obtained; therefore, no further substantial data for analysis from this area have been obtained.

We found that females were dominant (>80% of fish). This female dominance is not limited to the spawning area or the south-east Pacific Ocean: it also occurs in the feeding grounds in the Atlantic, Indian and south-western Pacific oceans (T. Itoh, unpubl. data). This is unusual in the Scombridae, in which the number of males and females is generally equal, or is otherwise skewed towards a higher proportion of males in the group of large individuals (Schaefer 2001). However, in wahoo (*Acanthocybium solandri*) there is a skew towards females (76%; Zischke *et al.* 2013). In large pelagic species (although not Scombridae), the swordfish (*Xiphias gladius*) and the blue marlin (*Makaira nigricans*) show a skew towards females in larger fish, and the sex ratio differs by area (Arocha and Lee 1996; Shimose *et al.* 2012). In the aforementioned studies, the proportion of males was higher in the spawning areas, at lower latitudes, suggesting that the distribution was segregated by sex and that males were resident in the spawning areas all year round. However, in the case of butterfly kingfish, the percentage of males in the spawning area was smaller than that of females; males accounted for <20% of fish in both spawning and feeding grounds. There are several possible reasons for this difference: the original number of males may have been small, male mortality may be higher or males may have been distributed in places where we did not sample. Regardless, further studies are warranted.

The sea surface temperature in the spawning area of the butterfly kingfish, between 14 and 18°C, was the second lowest of the Scombridae, next to that of the Atlantic mackerel (*Scomber scombrus*), which was between 5 and 23°C (Studholme *et al.* 1999). In all species except the slender tuna in the tribe Thunnini, including the genera *Thunnus*, *Katsuwonus*, *Euthynnus* and *Auxis*, spawning takes place at sea surface temperatures of ~24°C or higher. Reproduction at high temperatures permits high spawning rates, high reproductive output and rapid growth of offspring (Schaefer 2001). The spawning areas of fish in these genera are restricted to high-temperature regions, even though the adults of some of these species, such as the southern bluefin tuna, are well adapted to cold water, permitting them to exploit productive temperate waters. The butterfly kingfish may choose a different strategy, namely having a body adapted to cold water, with a brain heater and a thick fat layer beneath the scales (Collette *et al.* 2001); by spawning in cooler water, it avoids competition with the Thunnini in their early life stages.
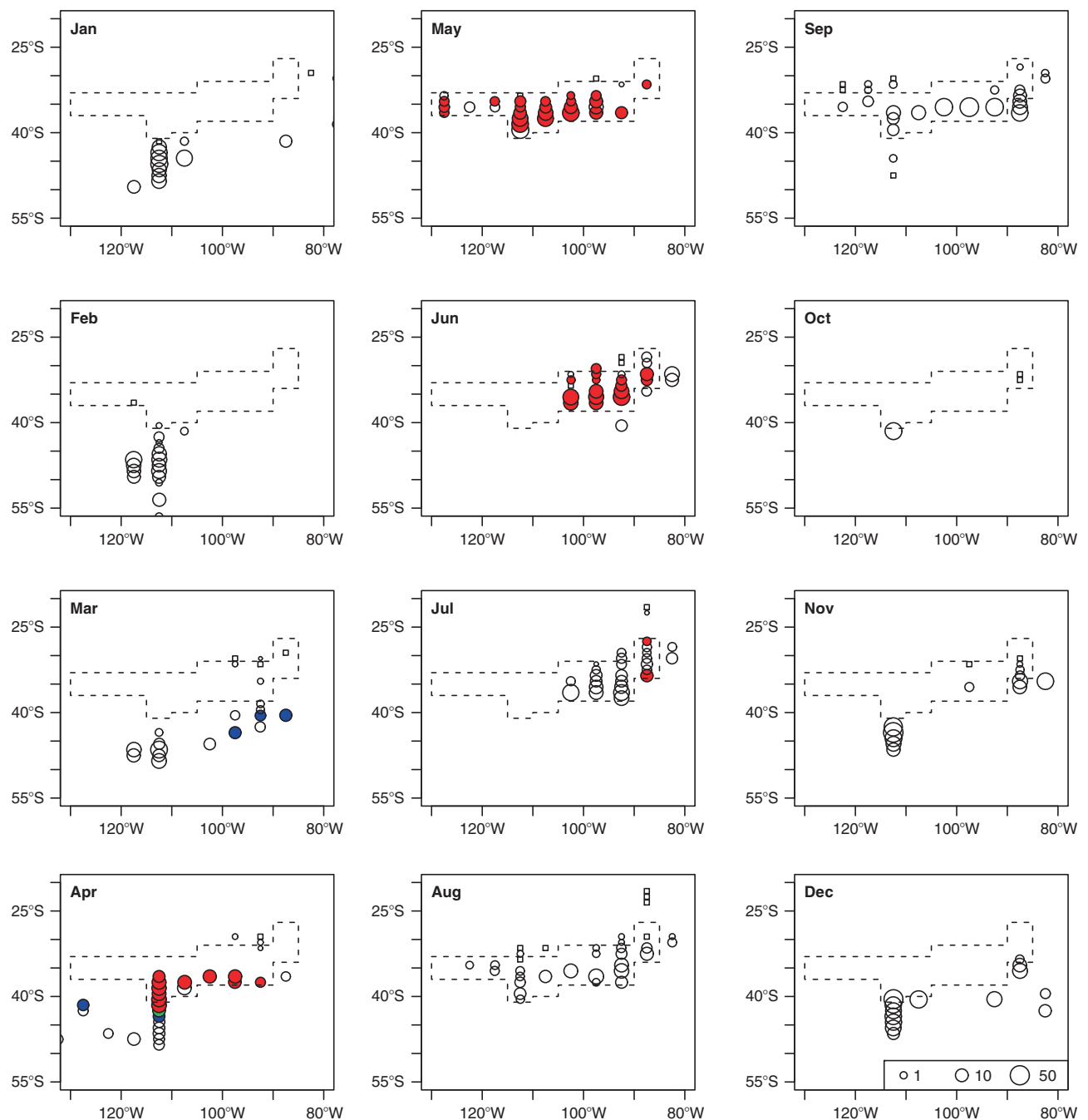
Fig. 7. Monthly distributions of butterfly kingfish catch and maturity. Polygons show the assumed spawning area. The size of the circles denotes catch per unit effort (CPUE; fish caught per 1000 hooks; see December panel). Squares represent zero catch. Red, green and blue denote female gonadosomatic indices (GSIs) of >5, 4–5 and 3–4 respectively. The colours of the highest GSIs of at least four females are shown.

The spawning area we delineated is located in the subtropical convergence zone. The whole range of the butterfly kingfish caught in the south-eastern Pacific was in the area between the North Subtropical Front and the Subantarctic Front (Belkin and Gordon 1996). The spawning area was in the lowest latitudinal part of this area, where the highest sea surface temperatures occur during the month in which spawning was observed.

A review of egg diameter in 288 pelagic species found that the majority were in the range between 0.6 and 1.6 mm (Ahlstrom and Moser 1980). In most Scombridae species, including *Thunnus* and *Scomber*, the diameter of hydrated eggs is ~1.0 mm (e.g. Fritzsche 1978; Studholme *et al*. 1999; Margulies *et al*. 2007), although Japanese Spanish mackerel (*Scomberomorus niphonius*) has an egg diameter of 1.6 mm

Table 2.   Summary of information on female butterfly kingfish with hydrated eggs in their ovaries
Egg diameter is presented as the mean ± s.d. of 100 eggs per fish

Fish	Date (1994)	Latitude (°S)	Longitude (°W)	Fork length (cm)	Bodyweight (kg)	Gonad weight (g)	Egg diameter (mm)
1	4 May	38	112	150	53	550	1.55 ± 0.07
2	19 May	37	108	178	110	5,050	1.74 ± 0.09
3	3 June	35	95	138	40	1,300	1.63 ± 0.09
4	8 June	35	96	163	80	1,400	1.74 ± 0.09
5	19 July	28	86	124	29	420	1.57 ± 0.07
Mean							1.64 ± 0.08
Standard error							0.042

(Yokogawa 1995). Therefore, at 1.6 mm in diameter, the hydrated egg of the butterfly kingfish is one of the largest among the Scombridae.

It has been hypothesised that the butterfly kingfish branched early on from the scombrid stem and underwent its own specialisations in morphology and distribution (Kohno 1984; Block *et al.* 1993). Spawning at lower temperatures, a large egg and female dominance are likely to be mutually related factors in the reproductive strategy of butterfly kingfish: larval survival rates are increased by the production of large eggs to compensate for the slow larval growth at low temperatures, and female dominance compensates for the fact that, if eggs are larger, then fewer are produced. This is an additional specialisation of the species.

Butterfly kingfish are also distributed in temperate waters of the Atlantic, Indian and south-western Pacific oceans in the Southern Hemisphere (Warashina and Hisada 1972). Fish in these areas are much smaller than in the south-eastern Pacific Ocean, ranging from 80 to 160 cm FL, with a length mode of ∼120 cm FL. Spawning, as evidenced by the finding of fish with fully developed ovaries, has not yet been shown to occur in these areas. There are areas other than the south-eastern Pacific Ocean that have sea surface temperatures in the range 14–18°C between April and June, but longline fishery data show that the number of butterfly kingfish caught in these areas is small and the CPUEs are low (T. Itoh, unpubl. data). It is highly likely that the south-eastern Pacific is the major spawning area of the species in light of the large catch number and high catch rate. Therefore, we consider that there is a single global stock of butterfly kingfish and that this fish migrates to the Atlantic, Indian and south-western Pacific oceans to feed, returning to the south-eastern Pacific Ocean to spawn. Note, however, that it is still unclear whether the spawning area is the only one or whether other (even small-scale) spawning areas exist. Examination of the ovaries of fish of this species from the Atlantic, Indian and south-western Pacific is warranted to resolve this question.

Conflicts of interest

The authors declare that they have no conflicts of interest.

Acknowledgements

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