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Changing relative abundance and behaviour of silky and grey reef sharks baited over 12 years on a Red Sea reef

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Abstract. There is a lack of studies on how provisioning may influence shark numbers and behaviour. The effects of long-term provisioning were investigated at a Red Sea reef, where both grey reef shark (*Carcharhinus amblyrhynchos*) and silky shark (*Carcharhinus falciformis*) occurred. Initially, grey reef sharks outnumbered silky sharks, but over 6 years, silky shark numbers increased almost 20-fold, whereas grey-reef sightings decreased >90%. Following this, silky-shark sightings also declined considerably (>80%). It is suggested that these declines could relate to local overfishing. Many silky sharks were identified individually through distinctive markings or conventional tagging. Some individual silky sharks were recorded regularly over 2 years or more, but most appeared to be transient visitors. Sighting records indicated that provisioning extended the residency of transient individuals. If visiting silky sharks were drawn from a larger regional population, this would explain both their initial accumulation and why, to begin with, sightings were sustained despite local fishing pressure. Conversely, the site fidelity typical of grey reef sharks would have made them more susceptible to local depletion. Silky sharks were recorded as behaving more boldly when present in greater numbers, but the decline in grey reef sharks appears to be unrelated to the initial increase in the numbers of silky shark.

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Introduction

Baiting, or provisioning, of sharks to attract them to sites where they may be observed or studied by SCUBA divers has become an established procedure (Carwardine and Watterson 2002). Over the past 10–20 years, shark-watching has become an increasingly common pastime (Gallagher and Hammerschlag 2011), generating significant revenue in several countries (e.g. Cline 2008; Vianna *et al.* 2012). However, the potential impacts of provisioning sharks in this manner remain largely uncharacterised, with existing studies reporting either negative effects or negligible effects (Laroche *et al.* 2007; Clua *et al.* 2010; Fitzpatrick *et al.* 2011; Maljković and Côté 2011; Hammerschlag *et al.* 2012). It is also unclear whether the numbers of sharks attending provisioning stations might be used to monitor local populations, or whether such provisioning might itself influence their local abundance. Nor has full consideration been given as to whether habituation of sharks to human presence might put either sharks or humans at greater risk of exploitation or injury. Consequently, concern persists that provisioning may alter shark condition, community interaction and compromise human safety (Newsome and Rodgers 2008). Here, data collected over 12 years on sharks visiting a baiting station on a coral reef in the Red Sea are assessed.

Two species were attracted to the baiting station, silky shark, *Carcharhinus falciformis*, and grey reef shark, *Carcharhinus amblyrhynchos*. Whereas the grey reef shark is regularly encountered at depths of 20–50 m around coral reefs, the silky shark is normally regarded as an oceanic or epipelagic species, being most common in continental-shelf waters more than 200 m deep (Compagno 2001). Consequently, whereas grey reef sharks are regularly seen on the upper reef slope by SCUBA divers, silky sharks are not often encountered by divers, save on reefs adjacent to deep water (Tricas *et al.* 1997). Hence, the two species are not often observed together, and how they may interact is unknown.

Both species are fast-swimming and agile predators (Compagno 2001; Compagno *et al.* 2005), but the silky shark grows larger than does the grey reef shark, i.e. up to 3.5 m in total length versus 1.9 m for grey reef shark. However, the grey reef shark is known for possessing, at least in some locations, a marked threat display (Johnson and Nelson 1973). The two species are also believed to differ in social organisation.

Individual grey reef sharks are described as showing strong fidelity to particular reefs, although some individuals may move over 100 km between less isolated reefs (McKibben and Nelson 1986; Heupel *et al.* 2010; Field *et al.* 2011). This fidelity is home-ranging rather than territorial, with the species tolerating conspecifics, and even gathering seasonally in groups of up to 20 or more (Nelson 1981; Clarke *et al.* 2012). In contrast, silky sharks show limited site fidelity, although they will aggregate around desirable food sources (Filmalter *et al.* 2011), where schools of up to 1000 individuals or more may form (Villegas and Sesana 2007).

Silky sharks, in recent decades, have been subject to very high mortality, especially because their association with tuna has resulted in large numbers being taken as a lucrative by-catch in long-line and purse-seine tuna fisheries (Compagno 2001; Watson *et al.* 2009; Filmalter *et al.* 2011). Similarly, grey reef sharks have shown sharp declines in abundance at many locations (Robbins *et al.* 2006; Graham *et al.* 2010). This is believed to have been the result of their exploitation in multi-species fisheries, combined with a susceptibility to local population depletion because of their site fidelity (McKibben and Nelson 1986; Heupel *et al.* 2010; Field *et al.* 2011). Consequently, there is increasing concern regarding the status of these species, with both now being classified by the IUCN as being *Near-threatened* (Bonfil *et al.* 2007; Smale 2009).

An understanding of the factors influencing the numbers of silky and grey reef sharks attending provisioning sites may be of value to efforts to manage or conserve their populations. Data collected over 12 years from the Red Sea baiting site were analysed, so as to assess whether the marked changes observed in the relative abundance of the two species over this time were the result of interspecific competition or the consequence of some other factor. Whether shark numbers varied consistently with season, and whether any seasonality might be related to reproductive cycle, were also investigated. With habituation of the sharks, close observation became possible, so that in many cases, individuals could be distinguished either by distinctive marks or the numbers on cattle ear-tags with which some individuals were tagged (Kohler and Turner 2001). This enabled investigation into whether individually identifiable silky sharks displayed similar visitation patterns and ranging behaviour.

Materials and methods

Study site and provisioning

The study site, where baiting and provisioning took place, was on a reef ~35 km south-west of Jeddah, Saudi Arabia, that has become known, as a result of the present work, as 'Silky Point' (21°16.272′N, 039°00.981′E). Silky Point is a no-entry zone, with access in principle possible only by special permission of the coastguard. The reef lies 10 km offshore and close to deep, open water, the sea bed dropping from a reef that breaks the surface at low tide, to a depth of over 600 m within only a few hundred metres (Fig. 1). The reef is ~0.5 km^2 and, on its western edge, has a steep slope with high coral cover from the surface to a narrow sandy plateau 20–30 m wide at 30 m, before dropping to depths of several hundred metres. The site has been visited by SCUBA divers from a private diving operation since 1995, after it was found to afford frequent shark encounters, both with grey reef and silky sharks. Since January 1998, Silky Point has been baited on a semi-regular basis, typically two or three times per week, conditions permitting, and normally observational data were recorded during each visit. Henceforth, the term 'baiting' is used here to describe the process of releasing into the water a mix of processed mackerel and tuna combined with tuna oil (placed frozen into a perforated drum moored at 10 m), typically followed by offering pieces of fish to sharks ('provisioning'), most commonly through hand-feeding with bonito (*Sarda* spp.). Approximately 5–10 kg of bait was taken underwater enclosed within one or more tubular plastic containers, from which pieces were taken in a controlled fashion to be made available to any sharks present.

Recording of observational data

Observational dives were performed by two experienced observers (normally including one of the authors) on SCUBA, with provisioning being undertaken from a platform structure fixed to the reef at 20 m depth. Each dive involved baiting of the site, followed by provisioning to any sharks present. Dives usually lasted ~30 min, with several parameters recorded during each, including the total number of individuals of each shark species present, sea-surface temperature (SST), sea state, horizontal underwater visibility, current direction and speed, and the number of divers in the water. Days without any documented shark sightings were included in the data record. Dives were typically performed 2–4 h after dawn and data recording began once divers had descended to a depth of 20 m. Typically, as a result of conditioning to the arrival of the boat, several sharks would be present before the divers entered the water. Visibility underwater was usually very good (25 m or more) and sharks that arrived usually remained mostly within view until provisioning was complete. Thus, it was normally not difficult to count the numbers of sharks present. Nevertheless, to minimise the risk of overestimation, the total number of sharks present was recorded as the maximum number observable at one time, except when it was evident that one or more individuals distinguishable by distinctive features (e.g. scars) were not included in this count, in which case these individuals were added in to the total.

The behaviour of the sharks was also recorded, with individuals being described as either 'cautious', 'relaxed' or 'bold'. A shark was classed as 'cautious' if it displayed any form of avoidance behaviour and/or kept its distance from the observers. A 'bold' shark would readily approach divers and take bait, often doing so by swimming erratically and at a higher rate, sometimes bumping into divers. If a shark was neither excitable, nor wary of diver presence, and showed generally slow swimming without any startle or avoidance response, and took bait in a calm manner, it was classed as 'relaxed'. The sex of each shark was also recorded, although this was often difficult when large numbers of individuals were present and if only the dorsum of the shark was seen.

For each dive, a form was completed that included drawing the observed markings onto a shark outline to facilitate consistency of identification among observers. If individual silky sharks showed distinguishing features, such as scars, pigmentation irregularities or injuries, these were noted, allowing repeat sightings of recognisable individuals to be recorded. It was also

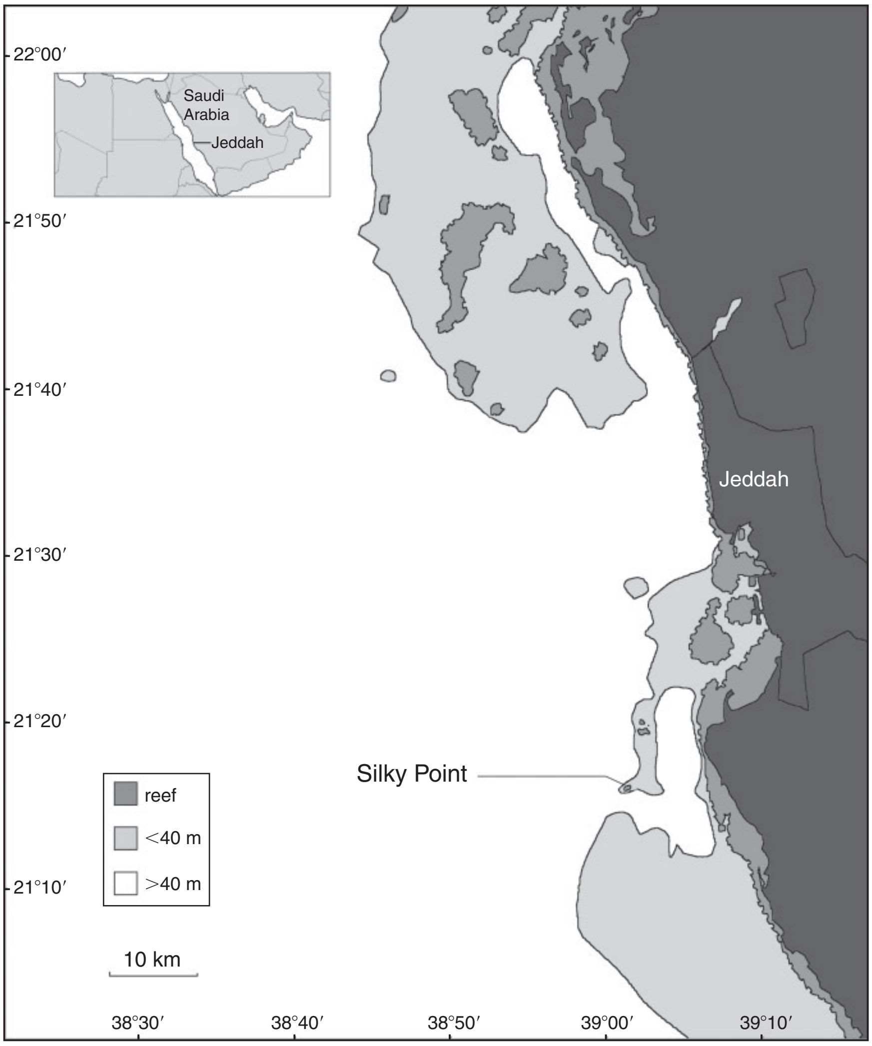

Fig. 1. The location of the study site, Silky Point, off the coast of Jeddah, Saudi Arabia, Red Sea, showing the coarse bathymetry of the area and the position of surrounding reefs.

recorded whether or not mature females were thought to be gravid; silky sharks are typically slender, so that when one displayed considerable abdominal bulging posterior to the pectoral fins, it was considered to be an indicator of a possible pregnancy. In addition, as indicated above, some individuals were tagged by inserting numbered nylon cattle ear-tags through the first dorsal fin (Kohler and Turner 2001), and these could often be read by divers who recorded the numbers. Tagging was performed underwater, after the sharks were restrained by hand; as they were taking bait, they were held by the upper caudal fin, which was firmly twisted so as to turn the shark onto its back, so inducing an apparent state of torpor similar to 'tonic immobility' (Henningsen 1994). This worked well on most individuals, although some proved less susceptible to the technique.

Data analysis

Varied weather conditions, manpower and boat maintenance limited the consistency with which the site could be baited. Consequently, to allow for weekly variation in baiting effort, and also to avoid the potential biasing effect of auto-correlation between successive daily data, the measure of abundance of silky and grey reef sharks used in statistical analysis was the mean number of sharks seen per dive over each 2-month period. This interval was determined through application to the daily data of an auto-correlation test (Minitab Release 15, Minitab, State College, PA, USA). Variation in mean numbers (over 2-month periods) both of silky and of grey reef sharks, with year, paired months, SST (bi-monthly mean SST), visibility (bi-monthly mean underwater horizontal visibility in metres), baiting effort (proportion of days per 2 months that baiting occurred) and with the mean number of the other shark species, was then tested using general linear models (Minitab Release 15). Prior to use in the GLM, the data were normalised through a $\log_{10}(x+1)$ transformation, although despite this measure, the distributions of the bi-monthly mean numbers of grey reef sharks did not quite obtain normality. Via economy of variables, the GLMs for both shark species were also reconstructed to include only the significant factors.

Data on sightings of individually recognisable sharks were used to assess both the frequency with which individual sharks

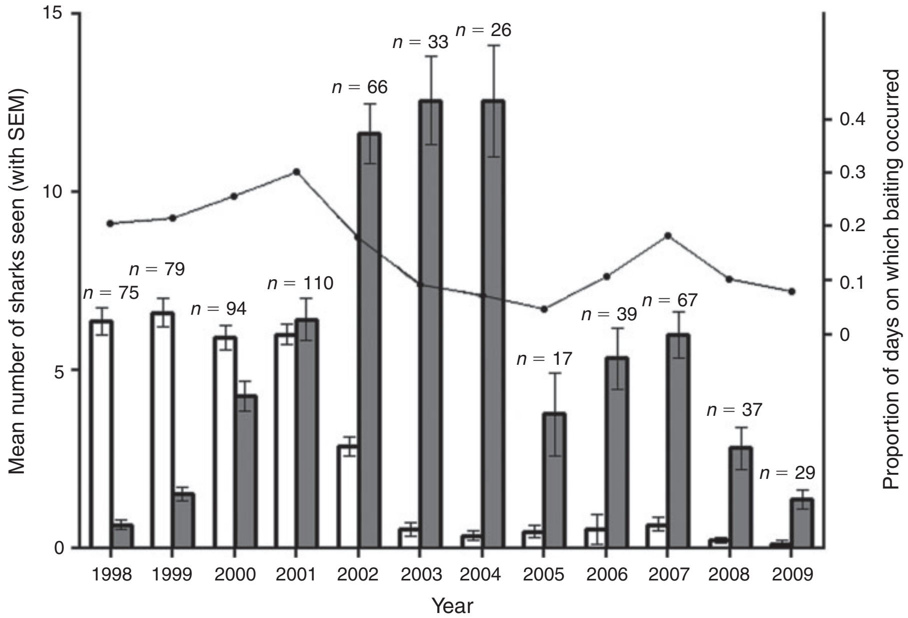

Fig. 2. Year-to-year changes in the mean numbers of sharks recorded (with s.e.m.), compared with variation in baiting effort. Shaded bars = silky sharks, unshaded = grey reef sharks, line = proportion of days in the year during which baiting occurred, *n* = the number of observation days for that year.

visited the site, and the total period over which they did so, by plotting for each identifiable individual the number of times that it was recorded, and also the time between the first and last sightings. How individually identifiable sharks modified their behaviour in response to the presence of others was investigated by plotting the mean number of other sharks present for each occasion on which individually identifiable sharks were recorded as appearing 'cautious', 'relaxed' or 'bold', with variation tested using a Kruskal–Wallis test (GraphPad Prism 5, GraphPad Software, La Jolla, CA, USA).

Results

Shark relative abundance

The two shark species normally encountered at Silky Point were the grey reef shark, *C. amblyrhynchos*, and the silky shark, *C. falciformis*. The only other shark species recorded was the whitetip reef shark, *Triaenodon obesus*, sightings of which were too rare to allow statistical analysis. The number of silky sharks present at the site ranged from 0 to 32 individuals (median 3), with the corresponding range for grey reef sharks being 0–16 (median 3). Initially, only low numbers of silky shark were encountered at the site (Fig. 2), typically only one or two per dive over the first 2 years (1998 mean was 0.66 sharks, with 65.3% of dives recording no silky sharks). Subsequently, however, between years 2000 and 2004, there was a 19-fold increase in the mean number of silky sharks present, peaking in 2003 and 2004 (Fig. 2), when more than 30 silky sharks could be present on a single dive (mean for 2003 of 12.55, with only 3.0% of dives without any silky sharks). However, during the second half of 2004, the mean numbers of silky shark seen per dive started to decrease, and from 2007 onwards, dives with more than 10 silky sharks were rare (mean 1.38 per dive in 2009, with 40–50% of dives with no silky sharks from 2008 onwards). Despite this trend, numbers still fluctuated markedly, with large numbers of silky shark still being encountered on some occasions in 2006 and 2007. Although more silky sharks were still encountered at the end of the study than at the beginning (in 1998), the reduction from the peak in 2003 to the numbers recorded in 2009 represented an 89.0% decline in the numbers present.

The pattern of change in the number of grey reef sharks contrasts markedly with that of silky sharks (Fig. 2). From 1998 until 2001, grey reef sharks were frequently encountered in high numbers (5–10 per dive, mean 6.36 in 1998, only 12.0% of dives without grey reef sharks) and, on most occasions, outnumbered silky sharks. But through 2002 and 2003, there was a sharp decline in the number of grey reef sharks, until sightings of more than two became uncommon, with the species being largely absent from 2008 onwards. An average of only 0.14 individuals were seen per dive in 2009, representing a 97.0% reduction in sightings since 1998, with 86.2% of dives in 2009 recording no grey reef sharks.

The outputs of the GLM (Table 1) indicated that variation in year, the interaction between year and 2-monthly period, SST and baiting effort were all significant predictors of the mean number of silky sharks at Silky Point, collectively accounting for 76.3% of the observed variation in numbers. Thus, the observed changes in the bi-monthly mean number of silky sharks deviate from the assumption of no change over time more than would be expected by chance alone. Baiting effort proved to be the most important predictor (Table 1). Neither the numbers of grey reef shark, visibility, nor time of year provided any explanatory power in the context of the other variables.

The similar GLM for the mean number of grey reef sharks found only year to be a significant factor, accounting for 93.3%

Table 1. Summary of the results of the general linear model for response variables against the bi-monthly mean number of silky and grey reef sharks at Silky Point (transformed using $\log_{10}(x+1)$)
SST = sea-surface temperature; significant *P*-values are in bold

Shark	R^2 (adj.)	Factor	d.f.	*F*	*P*
Silky	76.29	Bi-month	1	1.07	0.308
		Bait	1	10.69	**0.002**
		Grey reef	1	0.53	0.473
		SST	1	5.33	**0.027**
		Vis	1	0.93	0.340
		Year	11	5.08	**<0.001**
		Year × bi-month	11	2.66	**0.013**
Grey reef	93.33	Bi-month	1	0.05	0.824
		Bait	1	0.02	0.885
		Silky	1	0.53	0.473
		SST	1	0.01	0.904
		Vis	1	0.02	0.890
		Year	11	10.06	**<0.001**
		Year × bi-month	11	1.99	0.059

Table 2. Summary of the results of the general linear model for response variables against bi-monthly mean number of silky and grey reef sharks at Silky Point, after insignificant variables were excluded
SST = sea-surface temperature; significant *P*-values are in bold

Test	R^2 (adj.)	Factor	d.f.	*F*	*P*
Silky	76.59	Bi-month	1	1.16	0.289
		Bait	1	13.38	**0.001**
		SST	1	4.95	**0.032**
		Year	11	6.39	**<0.001**
		Year × bi-month	11	2.65	**0.013**
Grey reef	92.07	Year	11	68.52	**<0.001**

of the observed variation (Table 1). None of the other factors, even baiting effort, accounted for any significant portion of variation in the mean number of grey reef sharks (Table 1). As a further test, both GLMs were reconstructed to include only the significant factors; this increased the significance of both baiting effort and year for silky sharks, and likewise, indicated that for grey reef sharks, year alone accounted for 92.1% of the observed variation in mean numbers (Table 2). Although insignificant on its own, bi-monthly time of year was still included in the second silky shark model as a requirement of Minitab for including the year × month interaction term.

Thus, despite the temporal coincidence (Fig. 1) of peaking silky-shark numbers with decreasing grey reef shark numbers, the GLM showed no significant relationship between the bi-monthly mean numbers of the two species. A Spearman's rank correlation performed on the raw daily counts of the two species did show a weak negative relationship between the number of grey reef sharks present and the number of silky sharks present on any one day ($r = -0.100$, 95% CI $= -0.176 - -0.022$, $P < 0.01$). If only the maximum number of grey reef sharks for any number of silky sharks was considered, a stronger negative relationship was obtained ($r = -0.818$, 95% CI $=$ $-0.912 - -0.643$, $P < 0.001$), suggesting that on a day-to-day basis, the arrival of larger numbers of silky sharks may deter grey reef sharks from approaching the baiting station. However, there was no evidence for any significant effect of the mean local abundance of either species on the other, when considered in context with other variables (Table 1).

Baiting effort accounted for the majority of the variation explained by the silky-shark GLMs (Tables 1, 2), but the models accounted for only three-quarters of the observed variation in the numbers of silky shark. Although there was some lag, the growth in silky-shark sightings did follow the gradual increase in baiting effort, and, subsequently, for at least 2 years (2003, 2004), numbers of silky sharks remained very high, despite baiting effort dropping considerably (Fig. 2). When baiting effort was temporarily revived, the numbers of silky shark began to recover and reached a secondary peak after a couple of years. However, despite this renewed baiting effort continuing through 2006 and 2007, the numbers of silky shark did not return to the previous high numbers, but showed a further decline through 2008 and 2009, to eventually reach levels little higher than those observed at the start of the study. By contrast, the numbers of grey reef sharks showed little relationship to baiting effort, year alone accounting for the majority of variation in bi-monthly mean numbers of grey reef shark. This suggested that some factor unaccounted for in the present study, but correlated with the passage of time, strongly influenced the numbers of grey reef sharks.

Regarding seasonal variation, there was an apparent decline (but not absence) of both species during the summer (July–August), the period that coincided with the highest SST values. In addition, silky sharks showed a notable peak in numbers during spring (primarily during April–May; Fig. 3). At this time of year, SSTs are intermediate between the lowest (in late winter) and highest (in late summer) temperatures, so that there is no simple correlation between shark numbers and temperature. Patterns in monthly numbers of grey reef shark are less consistent, with peaks occurring in April and June, despite apparently lower numbers recorded in May and July. Although bi-monthly period as an independent factor proved insignificant in both GLMs, its interaction term with year was significant for silky sharks but not grey reef sharks (Table 1). This showed that for silky sharks, there is consistent intra-annual variation in attendance once the overriding long-term patterns of change have been accounted for, whereas numbers of grey reef shark did not significantly differ among months.

Silky-shark behaviour

Data on re-sightings of individual silky sharks and their behaviour have been used only from the onset of the study up until the end of 2002, because behavioural information was not recorded beyond 2002. All 30 silky sharks identified by markings and tags were female (Table 3), with individuals recorded on 22 March 1998, 23 March 1998, 16 April 1998, 19 March 2000 and 29 May 2000 suspected of being gravid. From over 3600 cumulative silky-shark sightings during the study, males were recorded only six times, with recordings occurring on 28 August 2000, 10 October 2000, 24 August 2001 (2) and 26 August 2001 (2). Mating was observed once at the feeding site, on 28 August 2000, a video of which is available (Video 1, available as Supplementary Material).

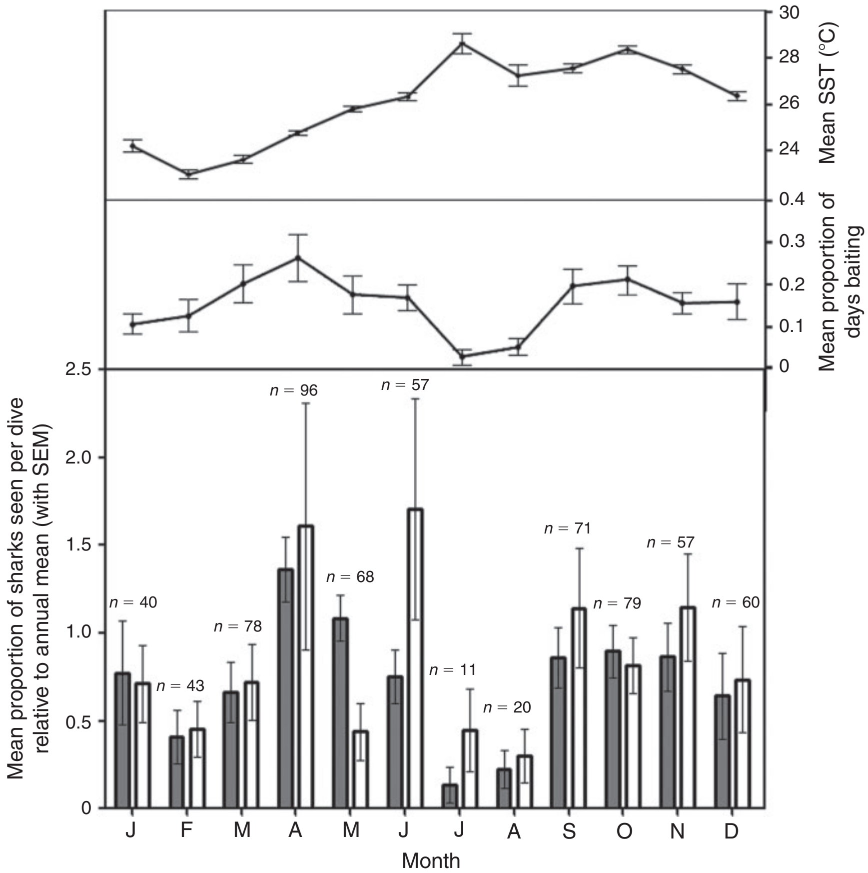

Fig. 3. Seasonal variation in the relative mean number of sightings per month (relative to the annual mean) of silky and grey reef sharks at Silky Point over 12 years from 1998 to 2009, compared with monthly mean sea-surface temperature and baiting effort. A value >1 indicates that the mean number of sharks seen that month was greater than the annual mean; a value <1 indicates that it was lower. Shaded bars = silky sharks, unshaded = grey reef sharks. Error bars show the standard error of the mean, n = the number of observation days for that month.

On comparing the number of different occasions on which each individually recognised silky shark was sighted with the overall time span over which these sightings occurred, there was found to be a strong skew in the data (Fig. 4). Four individuals (13%) were observed for over 12 months, whereas the majority (70%) was recorded at the site over only 2 months or less. This showed that the presence of most individual silky sharks at the site was relatively transient. Nevertheless, a few did show a long-term association with the site, with three of the sharks (A, D, J) being recorded over the course of more than 2 years, and one (A) being present throughout the 5 years of behavioural observations. In general, sharks that were around for longer tended to have more total sightings ($r = 0.795$, 95% CI = 0.602–0.900, $P < 0.001$), but there was marked variation around this correlation. Some individuals (e.g. 28 and K) that were around only transiently, were recorded as many times as was Shark D, which was seen only 13 times but over a 5-year period. Similarly, whereas Shark I was seen only five times over the course of 5 months, some others (e.g. 27–29) where seen 5–15 times in less than a month. Thus, some individuals appear to remain in the area for short or long periods, others perhaps visit irregularly.

Most individually recognisable silky sharks exhibited a full range of observed behaviours, being recorded as cautious, relaxed or bold on different occasions (Table 3). The relative frequencies of different behaviours did not differ substantially among identified sharks ($F = 1.30$, d.f. = 29, $P = 0.161$). It is of note, however, that on some occasions when there were multiple sharks present that they did tend to exhibit similar behaviour. The main trend, however, was that individually identified silky sharks tended to exhibit cautious behaviour if few other conspecifics were present, and bold behaviour if large numbers of conspecifics were present (Fig. 5, Kruskal–Wallis $H = 65.34$, d.f. = 24, $P < 0.001$). On average, the sharks showed cautious behaviour if fewer than four other individuals were present, relaxed behaviour with between five and seven other sharks present, and bold behaviour when 10 or more others were recorded (Fig. 5). Nevertheless, on some occasions, a shark acted boldly, even though few others were present (e.g. Shark B, 27 January 1999, with one other present), or cautiously when many were around (e.g. Shark 21, 4 April 2000, with six others present). At no point was any intraspecific aggression observed, nor was any aggressive behaviour experienced towards divers.

Table 3. Summary information for individually identified silky sharks, where numbers indicate sharks recognisable from cow tags attached to their first dorsal fin, and letters indicate sharks recognisable from distinctive physical marks or features

F = female, M = male, C = the number of times the individual was recorded being cautious, R = the number of times the individual was recorded being relaxed, B = the number of times the individual was recorded being bold

ID	Sex	First seen	Last seen	No. of sightings	C	R	B	Features
12	F	3 May 1998	3 May 1998	1	–	1	–	Tag
13	F	4 May 1998	4 May 1998	1	–	–	1	Tag
14	F	7 Dec. 1998	7 Dec. 1998	1	–	–	1	Tag
17	F	25 May 1999	25 May 1999	1	–	1	–	Tag
18	F	27 Mar. 2000	15 May 2000	9	–	4	5	Tag
20	F	3 Apr. 2000	22 May 2000	9	–	7	2	Tag
21	F	4 Apr. 2000	20 Apr. 2000	5	1	2	2	Tag
22	F	14 May 2000	14 May 2000	1	–	1	–	Tag
23	F	15 May 2000	7 June 2000	5	–	5	–	Tag
24	F	8 Apr. 2000	3 June 2000	9	1	7	1	Tag
25	F	14 May 2000	22 Apr. 2001	12	–	6	6	Tag
26	F	12 Apr. 2001	5 May 2001	10	–	3	7	Tag
27	F	10 Apr. 2001	19 Apr. 2001	8	–	5	3	Tag
28	F	10 Apr. 2001	3 May 2001	15	–	6	9	Tag
29	F	10 Apr. 2001	19 Apr. 2001	6	–	4	2	Tag
A	F	11 Mar. 1999 (1 Jan. 1996)[A]	20 Sep. 2003	38	4	19	15	Ring of discolouration around caudal peduncle
B	F	27 Jan. 1999	20 May 1999	7	–	3	4	Opaque left eye
C	F	20 Mar. 1999	21 Apr. 1999	5	1	2	2	Distinctive pigmentation on dorsal fin
D	F	11 Mar. 1999	24 Aug. 2002	13	1	5	7	Dark spots on the ventral surface
E	F	28 Feb. 1999	28 Mar. 1999	3	–	2	1	Malformed right pectoral and caudal fins
F	F	21 Apr. 1999	23 May 1999	3	–	2	1	Discoloured first dorsal (grey)
G	F	19 May 1999	25 May 1999	3	–	1	2	Missing tip of upper caudal
H	F	21 Nov. 1999	21 Nov. 1999	1	1	–	–	Unusually thin, marks on ventral surface
I	F	1 June 2000	14 Oct. 2000	5	–	4	1	Damaged rear left gill slits
J	F	29 Aug. 2000	24 Aug. 2002	17	1	11	5	Bent first dorsal
K	F	10 Sep. 2000	09 Nov. 2000	10	–	8	2	15 × 5 cm wound on upper caudal
L	F	10 Oct. 2000	14 Oct. 2000	3	–	3	–	Shredded edge of first dorsal fin
M	F	5 Nov. 2000	5 Nov. 2000	1	–	1	–	Discoloured patches behind left side of mouth
N	F	11 Sep. 2000	11 Sep. 2000	1	–	–	1	Notch in first dorsal fin, damaged left gill slits
O	F	10 Oct. 2000	14 Oct. 2000	3	–	2	1	Tear in first dorsal

[A]Shark A was identified on this date retrospectively from video footage.

Discussion

Changing relative abundance

Data were collected over a sufficiently long period for significant changes in the relative abundance of sharks to be evident, with GLM analysis indicating that for both species, the term 'year' accounted for significant portions of the variation in numbers attending the baiting station, indicating that, over time, there were significant changes in the numbers of shark present. Grey reef sharks predominated during the first 3 years, and their numbers were not strongly influenced by the frequency of baiting. Taken with the species' known restricted space use elsewhere (McKibben and Nelson 1986; Heupel *et al.* 2010; Field *et al.* 2011), this suggested a small local population (those with home ranges overlapping the site) that responded to bait, irrespective of how frequently baiting occurred. However, from 2001, their numbers declined by over 90%, to the point where only one or two individuals, if any, were seen. Over much the same period, the abundance of silky sharks at the site increased 10–20-fold. The silky shark is primarily an epipelagic offshore species, and the increase in its numbers at the site over 5–6 years may be interpreted as the steady accumulation of individuals with large, mainly pelagic, foraging ranges discovering and revisiting the feeding station. Subsequent to this, however, the abundance of silky sharks also declined considerably, by over 80% from the peak observed in 2003.

Similar gradual accumulation of sharks at provisioning sites, resulting in increased local abundance, has been reported for Galapagos sharks, *C. galapagensis*, and tiger sharks, *Galeocerdo cuvier*, in Hawaii, and bull sharks, *C. leucas*, in Fiji (Meyer *et al.* 2009; Brunnschweiler and Baensch 2011). Sharks can display strong associative learning abilities (Guttridge *et al.* 2009) and, at Silky Point, they appeared not only to associate the site with productive foraging but to respond to the arrival of the boat as a predictor of food, because sharks were often present before the application of any bait, as has also been reported for Galapagos sharks at provisioning sites in Hawaii (Meyer *et al.* 2009). Brunnschweiler and Baensch (2011) remarked that it remains undetermined how accumulating large predatory sharks in an area through provisioning may alter shark community dynamics, although Maljković and Côté (2011) reported that

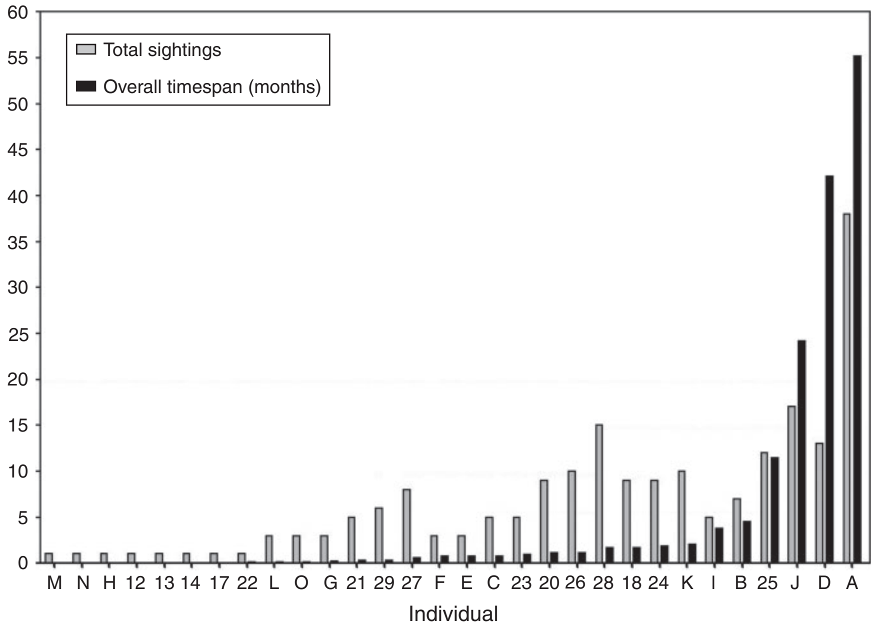

Fig. 4. The total number of sightings of each individually recognisable silky shark, compared with the time span over which it was recorded. Letters indicate individual sharks that were recognisable from distinguishing physical features, whereas numbers indicate sharks that were recognisable from numbered cattle tags attached to their first dorsal fin.

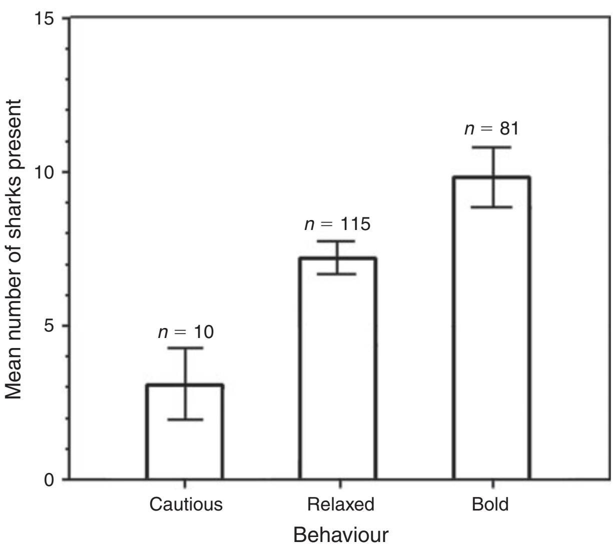

Fig. 5. The recorded behaviour of individually recognisable silky sharks, related to the number of other silky sharks present on baited dives from 1998 to 2002. Each bar shows the mean number of other sharks present with s.e.m. when any one recognisable individual showed bold, relaxed or cautious behaviour; $n =$ the number of times that each behaviour was recorded for any individual recognisable shark.

long-term provisioning of Caribbean reef sharks, *C. perezei*, in the Bahamas did not appear to have altered community structure or shark residency.

Nevertheless, the approximate coincidence of the contrasting trends in the numbers of silky and grey reef sharks was at first suspected to be the result of increasing numbers of silky sharks displacing or excluding grey reef sharks from the feeding site. At baited dives in Hawaii, increasing Galapagos sharks were thought to have caused declines in visiting sandbar sharks, *C. plumbeus*, through competitive exclusion (Meyer *et al.* 2009). The weak negative correlation between daily numbers of grey reef shark and numbers of silky shark could indicate a degree of competitive interaction for Silky Point. However, when the inter-annual variation was taken into account in the GLM, it was evident that the mean numbers of silky sharks present were not significantly related to the mean numbers of grey reef shark, implying that the main changes in abundance of the two species were not cause and effect. Closer inspection of the data provided further support for this conclusion. The numbers of grey reef sharks declined most during 2002 and 2003, when the numbers of silky sharks, although higher than before, were relatively stable (see Fig. 2), and there was no recovery in numbers of grey reef sharks from 2004 to 2009 when the numbers of silky shark declined to become comparable to those in 1999, the year after the provisioning began (Fig. 2). Thus, although there may have been some day-to-day behavioural interaction between grey reef and silky sharks, the increasing relative abundance of silky sharks does not appear to have driven the decline of grey reef shark.

Although emigration caused by other means remains a possibility, an alternative explanation for the decline in the numbers, first, of grey reef sharks and, then, of silky sharks is that they were both caused by fishing, the impact of which is likely to have been exacerbated by the sharks aggregating at the baiting site and responding even to boats approaching the site. Severe declines in abundance (over 90%) in response to fishing pressure have been reported for reef sharks on the Great Barrier Reef (Robbins *et al.* 2006) and the Chagos Archipelago

(Graham *et al.* 2010), as well as for silky sharks in the Gulf of Mexico (Baum and Myers 2004). The inshore waters of the Saudi Arabian Red Sea are heavily exploited by artisanal fishermen, who use hand-lining in reef areas to target predatory species such as groupers (Serranidae) and snappers (Lutjanidae) (Morgan 2004). Not only are sharks a by-catch in these artisanal fisheries, but during the latter part of the study, some dedicated shark-fishing vessels were present, exploiting what is currently one of the most profitable fisheries in the Red Sea (Spaet *et al.* 2012). Most of the catch is sold locally, with some of the larger individuals auctioned for export. During the study period, grey reef and silky sharks, as well as other shark species, were common at the fish market in Jeddah (although a significant proportion were understood to have been caught further south, e.g. near Jizan, J. Lea, pers. obs.). It was because of such fishing activity that the provisioning site was established in a restricted-entry area that boats could, supposedly, enter only with special permission. Nevertheless, fishing boats ignoring, or ignorant, of this regulation were observed in this area and were witnessed actually catching sharks close to the baiting site on more than one occasion (C. Clarke, pers. obs.). Further, baited hooked lines suitable for catching sharks were recovered from Silky Point on several occasions, and in the later stages of the study, silky sharks often carried hooks and leaders trailing from their mouth, or netting scars on their body.

If, as both observational and population genetic data suggest (McKibben and Nelson 1986; Heupel *et al.* 2010; Horn *et al.* 2010; Field *et al.* 2011), grey reef sharks principally occur as small resident populations with comparatively restricted movements, then it is plausible that, subjected to such sustained local fishing activity, the numbers in a particular reef area may be depleted quickly. This appears to have happened on unprotected reefs on the Great Barrier Reef, in Chagos and on the Mesoamerican Barrier Reef (Robbins *et al.* 2006; Graham *et al.* 2010; Bond *et al.* 2012). By contrast, although populations of silky shark have elsewhere been depleted by intensive pelagic fisheries (Baum and Myers 2004), because the animals roam mostly offshore, a population decline caused by inshore reef-based fisheries would be expected to take longer. Although the reduction in the frequency of baiting that took place during 2003–2005 may have contributed towards the initial decline in the numbers of silky shark after 2004 (Fig. 2), as demonstrated by its predominant significance in the GLMs (Tables 1, 2), when provisioning was intensified again during 2006 and 2007, there was only a limited recovery in numbers attending the site. This suggests that by this time, local fishing had also caused a decline in the numbers of silky shark.

Visit patterns

Although baiting effort influenced the numbers of silky shark, the GLM indicated that numbers also varied significantly across months. The April peak might have reflected a tendency for more diving and provisioning to be undertaken in April, when weather conditions were more favourable than at other times of year. However, there was no comparable increase in counts in September and October, when weather conditions were also favourable and similar amounts of provisioning were undertaken. These results suggest that, for some reason, silky sharks tend to visit reef areas more during late spring. This impression is consistent with studies at some other provisioning sites where sharks also retained their seasonal pattern of occurrence despite, in some cases, an increasing overall abundance (Meyer *et al.* 2009; Brunnschweiler and Baensch, 2011; Hammerschlag *et al.* 2012). By contrast, the numbers of grey reef sharks observed, although declining over the years, showed no consistent variation with time of year, a finding that would be consistent with their presumed residential behaviour.

The observation of strong sexual segregation of silky sharks at Silky Point and that peak numbers occurred in April when both daylength and water temperature are increasing suggested that the occurrence of females on the reef at this time may be related to reproductive activity. Gravid females were observed only between March and May, and it is possible that such reef habitat may be favoured for gestation and/or parturition. Similar use of reef banks by silky sharks for parturition has been reported to occur in the Gulf of Mexico (Bonfil *et al.* 1993). However, studies of the reproductive organs of silky shark have supported contrasting conclusions on seasonality of breeding, some suggesting that reproduction takes place seasonally (Branstetter 1987), others that it occurs throughout the year (Bass *et al.* 1973; Stevens and McLoughlin 1991; Bonfil *et al.* 1993; Hazin *et al.* 2007; Hall *et al.* 2012). A plausible interpretation is that at higher latitudes, pupping takes place seasonally, whereas at lower latitudes, where water temperatures are more consistent, it may take place throughout the year.

Whether or not pupping occurs in reef areas, some of the individually recognisable female silky sharks were observed at the provisioning site through much or all of the year, and in a few cases, over several years. This indicated that some females may make more general use of reef areas, particularly, where these occur adjacent to deep water, perhaps to forage for reef-associated food, or possibly to avoid unwanted attention from males, given the associated costs of mating (Pratt and Carrier 2001). Conversely, many other individuals were observed on relatively few occasions or over only a short period of time following the first recording. This latter pattern is consistent with most individuals roaming over large sea areas, and perhaps visiting reefs only on an infrequent basis. Some silky sharks most frequently observed at the baiting station may, nevertheless, even make use of a sizeable home range, larger than those of grey reef sharks, because a few of the individually recognisable individuals were also recorded at a second reef site, ~50 km away, where provisioning also took place on a trial basis (Clarke *et al.* 2011). The data presented here are consistent with those from a parallel acoustic-tracking study (Clarke *et al.* 2011), which also suggested that some individuals may show ranging behaviour different from that of others, with perhaps different portions of the population pursuing alternative foraging strategies.

Silky-shark behaviour

The expression of bold behaviour has been found to be context dependent in several different species, including pumpkinseed sunfish, *Lepomis gibbosus* (Coleman and Wilson 1998), bighorn sheep, *Ovis canadensis* (Réale *et al.* 2000), three-spined sticklebacks, *Gasterosteus aculeatus* (Ward *et al.* 2004), and dumpling squid, *Euprymna tasmanica* (Sinn *et al.* 2008). Likewise, the silky sharks in the present study were not found to be universally cautious, relaxed or bold, but to display context-dependent variation in bold behaviour. The data showed that the degree to which the behaviour of identifiable silky sharks appeared bold depended primarily on the numbers of conspecifics present, with individuals showing increasingly bold behaviour, the greater the number of other silky sharks present. The function of agonistic displays by grey reef sharks remains uncertain, but they are considered a potential dominance signal directed towards both conspecifics and other species (McKibben and Nelson 1986; Martin 2007). However, no dominance signalling was observed among silky sharks at Silky Point; it may be that if most silky sharks move independently over large ranges, only sometimes forming aggregations around desirable food sources (Villegas and Sesana 2007), there may be little requirement for dominance signalling. Instead, the data suggested that silky sharks may be cautious in a novel situation when more or less alone, but more confident when the presence of conspecifics signals that the risk of the situation is acceptable. Such dilution of risk effects has been reported for starlings, which modify their foraging behaviour in the presence of conspecifics (Fernández-Juricic *et al.* 2004). Dilution of risk may be an adaptive basis of the observation that regular provisioning can result in sharks accumulating and showing increasingly confident behaviour (e.g. Clua *et al.* 2010).

Study limitations

The present study, although carried out over 12 years, was limited in its scope by several factors. At several points, attempts were made to provision the experimental site on a more consistent basis; however, this proved impractical because of logistical and manpower constraints, as well as sometimes unfavourable sea conditions. A second difficulty was that, as noted by Brunnschweiler and Baensch (2011), error in visual counts may result from counting the same individuals multiple times; this may especially happen when there is a lack of distinguishing marks on sharks of similar size. To mitigate this effect, the maximum number of sharks in view at one time was used as the recorded count, unless there was a good reason to add in more individuals. A related issue is that variable visibility on dives may influence the number of sharks counted. However, no effect of visibility on the number of sharks observed was evident in the present study, probably because the silky and grey reef sharks attracted by the bait tended to approach and remain closer than the poorest visibility encountered.

Concluding remarks

The present study showed, over 12 years, large declines in the numbers of both grey reef and silky sharks attending a provisioning site in the Red Sea. The numbers attending the site cannot be taken as a precise reflection of the species abundance in the region, but, given the consistency of procedure, must reflect their relative abundance in the locality of the baiting station. The reduction in grey reef sharks was particularly severe and seemingly long term, and unrelated to baiting frequency. Silky-shark abundance, although also greatly eventually reduced, is more difficult to interpret, because of the more vagrant pelagic behaviour of these sharks and the evident influence of bait availability. Nonetheless, the patterns of sharply declining abundance of both species are of significant concern and potentially attributable to local fishing pressure.

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