Reproductive characteristics of slipper lobster, cuttlefish and squid species taken as byproduct in a tropical prawn trawl fishery

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Reproductive characteristics of slipper lobster, cuttlefish and squid species taken as byproduct in a tropical prawn trawl fishery

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Abstract Reproductive characteristics relevant to population sustainability were examined for eight abundant invertebrate species caught as byproduct by the Northern Prawn Fishery (NPF) in northern Australia. Slipper lobsters *Thenus parindicus* and *Thenus australiensis* differed in their size at maturity, with *T. parindicus* maturing at smaller size. Both species had similar reproductive seasonality, with most recruitment early in the year (January–March). Our estimates of carapace length (CL) at which 50% of females are mature (CL_{50}) suggest that current management regulations (minimum legal size 52 mm CL) for *Thenus* are probably adequate for *T. parindicus*, but suboptimal for *T. australiensis*. However, *T. australiensis* only contributes a small proportion to the NPF *Thenus* catch. This species is likely to be protected as its preferred habitat is coarse substrate and deeper water (>40 m), which does not overlap greatly with the current commercial trawl effort distribution. *Uroteuthis* squid and *Sepia* cuttlefishes also varied in size at maturity and reproductive seasonality. Squid and cuttlefish populations are likely to be underexploited based on historical catches. Under current fishing levels, squid stocks appear to be resilient to the opportunistic targeting of spawning aggregations in similar NPF regions over several years.

Keywords Northern Prawn Fishery · GSI · Spawning aggregation · Fisheries management · *Uroteuthis* · *Sepia* · *Thenus*

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Introduction

Commercial fishing in many countries is now regulated by a complex combination of fisheries and environmental legislation. Markets and public perception have changed, with increasing expectation for fisheries to demonstrate that they are operating in an ecologically sustainable manner [1, 2]; for example, the Australian Fisheries Management Authority (AFMA) was required to assess all federally managed fisheries for their compliance with the Commonwealth's Environment Protection and Biodiversity Conservation (EPBC) Act 1999. This act requires that fisheries demonstrate that their impacts on target, byproduct, bycatch and threatened, endangered and protected species are ecologically sustainable.

The Northern Prawn Fishery (NPF) is Australia's largest prawn trawl fishery. This fishery was assessed under the EPBC Act in 2003. This assessment recommended the development and implementation of harvest strategies and a spatial management system for all target and byproduct species by 2008. For the NPF to demonstrate that they are operating in an ecologically sustainable manner the fishery has to implement the AFMA harvest strategies for all target and byproduct species. This requires accurate species-specific life history information to better understand the impacts of fishing on stocks. While there is good biological understanding of the targeted penaeid prawns [3–5], very little is known of life history traits for the numerous byproduct species caught in the NPF.

Size at sexual maturity, seasonal reproductive productivity, spawning sites, fecundity and growth rates are some of the most important life history information needed for stock assessment and sustainable exploitation of marine animals [6]. It is important to understand the timing of reproduction and recruitment of a fished population to produce management strategies that avoid overfishing [7]; for example, recruitment overfishing is of particular concern for squid populations which consist of new recruits annually [8]. Currently the limited life history information for byproduct species in the NPF makes it difficult to develop management plans that ensure their sustainability.

The NPF catches several byproduct groups, including slipper lobsters (*Thenus* spp.—commonly known as bugs), loliginid squids (*Uroteuthis* spp.) and sepiid cuttlefishes (*Sepia* spp.). Input controls are the primary management strategy used for this fishery. These include limits on the number of trawlers (52 since 2010), restrictions on gear used (size, number and type of demersal nets) and spatial and temporal restrictions on fishing operations. The spatial and temporal closures have been chosen based largely on the biological characteristics of the main target prawn species: the tiger prawns *Penaeus esculentus* and *Penaeus semisulcatus*, and the banana prawns *Penaeus merguiensis* and *Penaeus indicus*. Management measures for some byproduct also exist in the NPF. For slipper lobsters *Thenus*, there are two measures. There is a minimum legal size (MLS) of 75 mm carapace width ($\sim$52 mm carapace length) and a prohibition on retaining egg-bearing females [9]. These restrictions are based on biological parameters associated with yield optimization [10]. Under these restrictions, slipper lobsters should reach reproductive age and spawn at least once prior to capture [10].

In contrast, management restrictions for squid are not based on biological data; for example, the catch of squid is currently limited to the total weight of prawns reported by the fleet each year. Since 2006, the AFMA has set an annual 500 t interim limit reference point or 'trigger limit' for squid. If this total catch is reached then a review of management arrangements for squid will be conducted. There are no restrictions on the retention of cuttlefish.

For the slipper lobsters *Thenus*, there have been few detailed studies of their reproductive characteristics. Courtney [10] and Jones [11] summarised the most detailed studies from north-eastern Australia. These provided information on growth, longevity, maturation, fecundity and seasonal catch. The taxonomy and reproductive characteristics of the squid and cuttlefish species in northern Australia are poorly known [12–14]. Preliminary genetic studies in the early 1990s have shown the Australian squid taxa to be different from similar species in southeast Asia [14]. The two most abundant squid species, *Uroteuthis* sp. 3 and *Uroteuthis* sp. 4, occur across northern Australia [14].

This study was undertaken to: (1) identify size at maturity and examine spatial and temporal variation in reproductive condition for species in the three most economically important byproduct groups caught in the NPF, (2) describe some reproductive characteristics of a known squid spawning aggregation and identify other possible spawning aggregations based on commercial logbook catch records, (3) consider species-specific reproductive characteristics in relation to current management measures and fishing activity, in order to aid sustainability assessments and (4) discuss alternative management measures.

Materials and methods

Field sampling

Between August 2002 and July 2007, byproduct samples (slipper lobsters, squid and cuttlefish) were collected aboard commercial prawn trawlers on fishery-independent prawn population monitoring surveys [15]. These surveys were generally undertaken twice a year, the first in January–March (wet season) where approximately 200 sites are sampled and the second in June–August (dry season) when approximately 300 sites are sampled (Fig. 1). Samples were also collected from additional surveys conducted from September to October in 2003 and October 2004 (dry season). The sampling sites were allocated among six geographic regions based on commercial prawn trawling effort: Weipa, Karumba, Mornington, Vanderlins, south Groote and north Groote. Within regions, the locations of trawl sites were stratified by depth. Each site was trawled for a period of 30 min at 3.2 knots. Trawls were conducted at night to mirror commercial operating hours. For consistency, vessels used twin 'Florida Flyer' nets, each with a 12-fathom headrope, 2-1/4 inch diamond mesh and a codend of 120 meshes long and 150 meshes round (1-7/8 inch codend mesh size). A straight bar top opening turtle excluder device (TED) was used in each net. After each trawl, all slipper lobsters (*Thenus* spp.) were identified to species, and total weights and numbers were recorded for each net. Up to 100 slipper lobsters of each species were measured (carapace length, CL in mm) per trawl, and their sex and egg-bearing condition recorded. All squid and cuttlefish were counted, weighed onboard and frozen for further laboratory analysis.

Slipper lobster measurements

The length at sexual maturity (CL_{50}) of female lobsters, of both species, was defined from the size at which they became egg-bearing. It was estimated by fitting a logistic function with the equation

$$y = \frac{1}{1 + \exp(-k(\mathrm{CL} - \mathrm{CL}_{50}))}, \quad (1)$$

where y is the proportion of mature individuals (egg-bearing females) by carapace length, k is the parameter

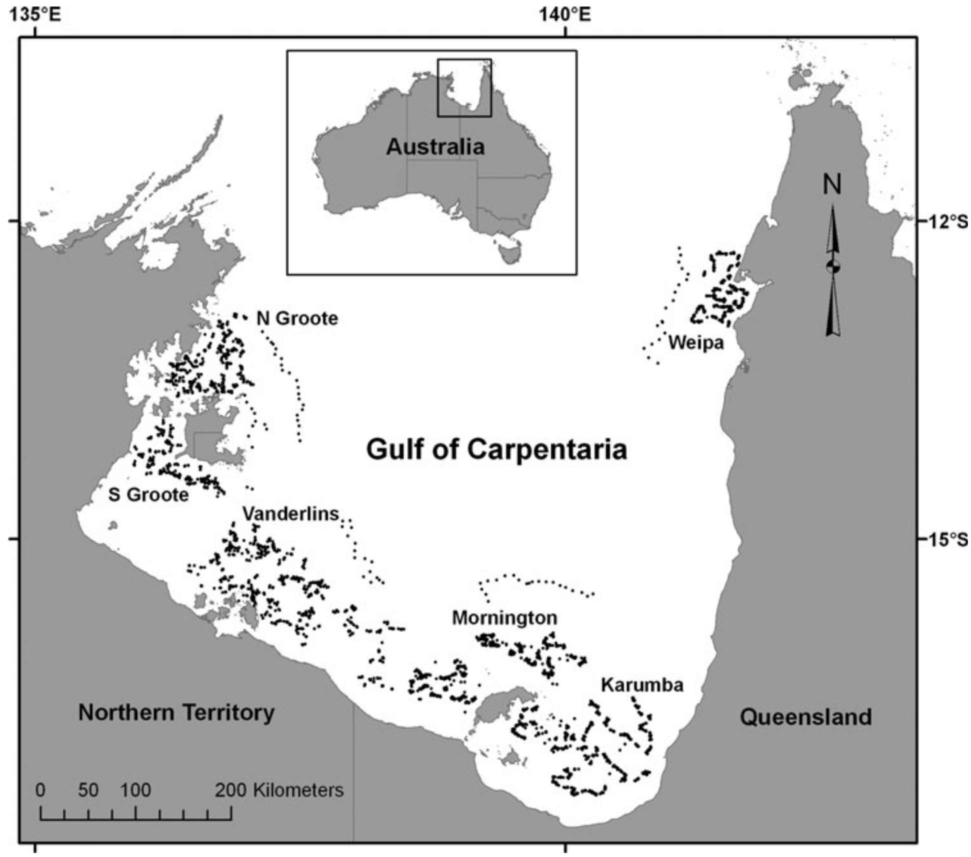

Fig. 1 Map of the Gulf of Carpentaria, showing the location of the fishery-independent trawl survey sites (*filled circles*) sampled for byproduct life history studies between 2002 and 2007

determining the slope of the maturity curve and CL_{50} is the estimated carapace length at 50% maturity (Fig. 2).

Squid and cuttlefish measurements

We processed a proportion of trawls, stratifying by region, season and year. For the trawl catches examined, we identified and dissected all squid and cuttlefish caught. Identification of squid and cuttlefish species was based on taxonomic descriptions provided by [13] (cuttlefish) and [14] (squid). Specimens were measured (dorsal mantle length, ML in mm), weighed (±0.001 g) and sexed, and gonads (ovary/testis) removed and weighed. The gonado-somatic index (GSI) was calculated with the following formula:

$$\mathrm{GSI} = (\text{gonad weight}/(\text{body weight} - \text{gonad weight})) \times 100. \tag{2}$$

Biological sampling and commercial catches of squid aggregations

Anecdotal information from fishers and fleet masters from NPF fishing companies suggested that most squid catches reported in the commercial logbooks were taken from spawning aggregations. To verify the logbook records and assess the species composition and reproductive status of squids caught in large aggregations, we examined a 20-kg subsample taken by an AFMA scientific observer onboard a commercial trawler that found a large squid aggregation in May 2007. The subsample was sent to the Australian Commonwealth Scientific and Research Organisation (CSIRO) and processed in a similar manner to other scientific samples. Commercial logbook records (available from 1998 to 2007) were also examined to assess the spatial and temporal variation in catches of >400 kg of squid day^{-1} in order to assess the predictability of these aggregations.

Spatial and temporal variation in spawning

The proportion spawning of each species was estimated from the number of sexually mature females with hydrated eggs (cephalopods) or egg-bearing (slipper lobsters). For cephalopod species, size at 50% maturity was determined by fitting a logistic model (Eq. 1) to the mantle length and GSI data using the SAS NLIN procedure (Fig. 3). Macroscopic examination of the ovaries of females of each

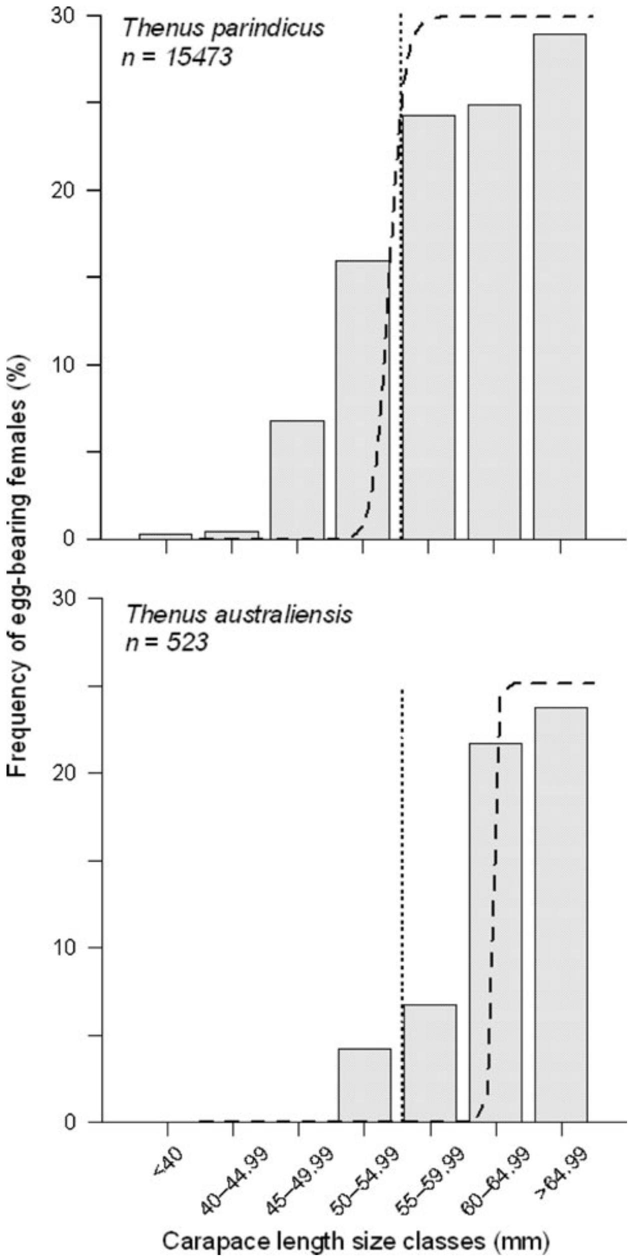

Fig. 2 Percentage of egg-bearing female *Thenus* slipper lobsters in each size class from samples collected between 2002 and 2007. The *vertical dotted line* is the minimum legal size that is allowed to be retained in the NPF. The *dashed curve* shows the mean logistic regression best fit

species defined as mature by this criterion confirmed that all individuals had enlarged and ripening eggs. The size at maturity was then used to determine the number of potentially mature females in the sampled population of each region (Karumba, Mornington, Vanderlins, north Groote, south Groote, Weipa) and season (wet, January–March; dry, June–October) over the 6-year sampling period (2002–2007). The percentages of mature females of each species in spawning condition were estimated by the following criteria: (1) cuttlefish with hydrated eggs or GSI >2.5% and (2) squid with hydrated eggs or GSI >5%. Individuals for each cephalopod species with these GSI values were observed to have large hydrated yellow eggs. We assumed that this represented an indicator of spawning condition. For slipper lobsters we used the estimated size at maturity (CL_{50}) to determine the number of mature individuals by region and season. The proportion of spawning females of the mature population was then determined by those that were egg-bearing.

Results

Overall catch

A total of 191,411 slipper lobsters, squid and cuttlefish were collected over the 6 years (Table 1). Of these, 13,693 were identified to species and examined for GSI, sex and length–weight relationships. Slipper lobsters were readily identified in the field and represented the most numerous species examined. Cuttlefish were the most abundantly caught species group, but the need to examine them internally for species identification reduced the number identified (Table 1).

Seasonal spawning pattern

The seasonal spawning pattern of slipper lobsters showed a similar cycle for the two species (Fig. 4). However, *T. parindicus* generally had a higher percentage of egg-bearing females, particularly during February and March (late wet season). The percentage of egg-bearing females of both species was highest late in the dry season (August–October), when almost 50% of the mature female population were carrying eggs. Both species appear to have an extended spawning season where egg-bearing females were detected through the year (Fig. 4). The exception to this was for *T. australiensis*, where there were few females caught ($n = 18$) later in the wet season (March) and none were egg-bearing.

The spawning season for the squid and cuttlefish species also appears to be extended for several species (Fig. 5). Mean GSIs were higher later in the dry season (August–October) for both *Uroteuthis* species, particularly for *Uroteuthis* sp. 4, and *Sepia smithi* and *S. papuensis*. The seasonal pattern of reproduction was less clear in the other two species of cuttlefish (*S. elliptica* and *S. pharaonis*), with a similar mean GSI throughout the year (Fig. 5). There was evidence that spawning might also be occurring in the wet season for some species (*Uroteuthis* sp. 3, *Sepia elliptica*, *S. smithi* and *S. pharaonis*). Unfortunately, no samples were collected between April and June (dry season).

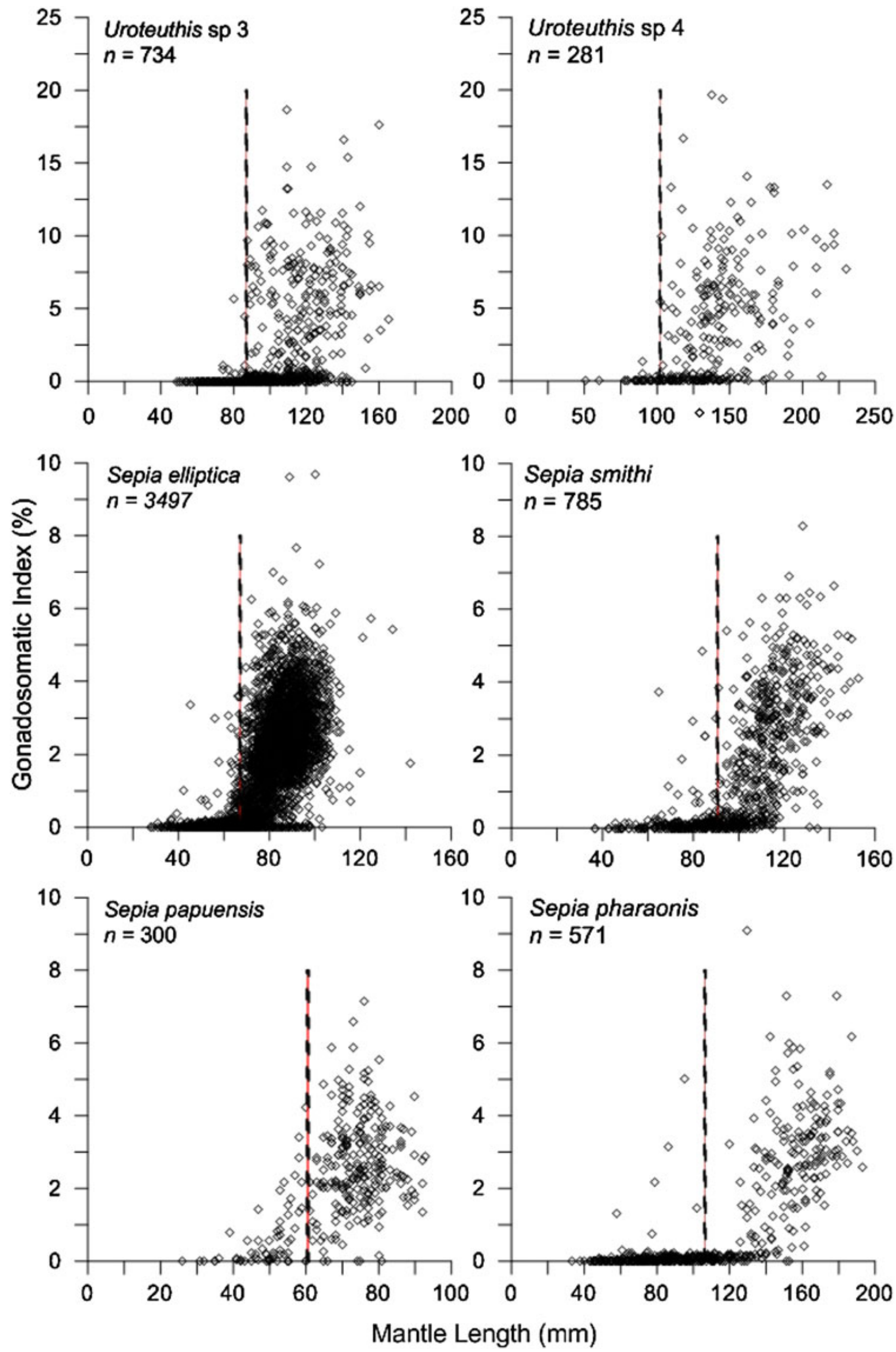

Fig. 3 Female gonadosomatic index (%) of two species of squid and four species of cuttlefish caught in the Gulf of Carpentaria from August 2002 to July 2007. The *dashed vertical line* indicates the estimated size at 50% maturity determined by fitting a logistic model

Commercial catches from the squid spawning aggregation subsampled in May 2007 were from west of Mornington Island in the Gulf of Carpentaria where the water depth ranged from 22 to 27 m (Fig. 6). All squid examined were identified as *Uroteuthis* sp. 4. In total, 119 adult squid weighing 7.3 kg were processed. These comprised 57 males and 62 females (M/F ratio 0.92). Female GSIs varied widely (Table 2), with some specimens clearly spent and suffering some mantle muscle degeneration. Egg capsules were detected among the squid samples, and spermatophore bulbs were evident in the buccal pouches of the females, indicating that mating and spawning were occurring at the same time. There were two modal sizes of the males, with all specimens mature and dominant among the

Table 1 Summary of total number of byproduct specimens collected in the Gulf of Carpentaria and processed for reproductive characteristics from August 2002 to July 2007

Byproduct group	Common name	Species	Collected at sea	Laboratory processed
Slipper lobsters	Mud bug	*Thenus parindicus*	127,308	240
	Reef bug	*Thenus australiensis*	3,127	8
Squid[a]	Broad squid	*Uroteuthis* sp. 3		2,433
	Slender squid	*Uroteuthis* sp. 4		816
Cuttlefish[a]	Ovalbone cuttlefish	*Sepia elliptica*		6,981
	Papuan cuttlefish	*Sepia papuensis*		571
	Pharaonis cuttlefish	*Sepia pharaonis*		1,129
	Smith's cuttlefish	*Sepia smithi*		1,553

[a] Species could not be identified at sea

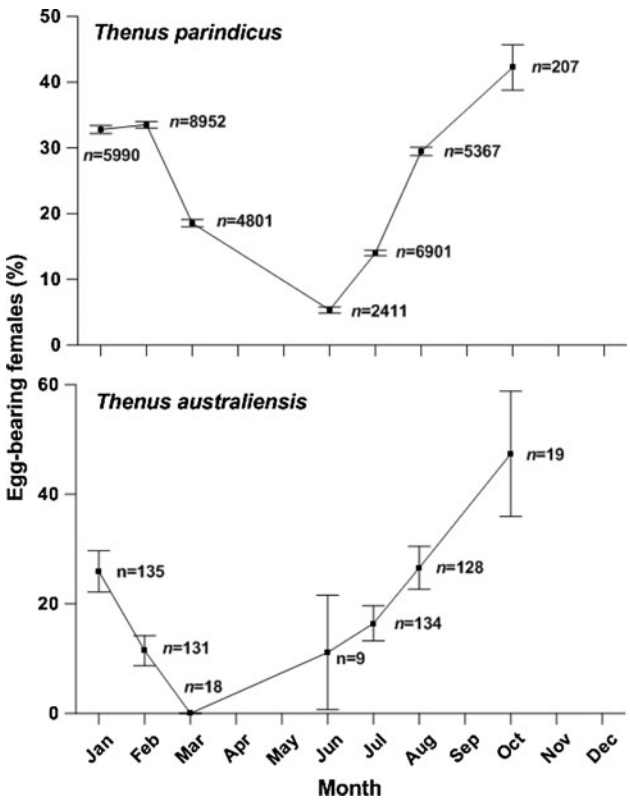

Fig. 4 Mean percentage ± 95% confidence limit of egg-bearing females of two species of slipper lobster caught in the Gulf of Carpentaria from August 2002 to July 2007

larger size classes (Fig. 7). Several other large catches of squid were recorded in commercial logbooks in May near Mornington Island (Fig. 6). Large catches later in the year (September–October) were also made further west, around Groote Eylandt. The occurrence of these aggregations appears to be relatively predictable, as large catches were made in the same area in May 2001 and 2002.

Slipper lobster sexual maturity

The dorsal carapace length of mature female *T. parindicus* ranged from 34.5 to 81.5 mm, and from 52.7 to 89.5 mm for *T. australiensis*. The mean estimated carapace length of females at sexual maturity (CL_{50}) was 52.0 ± 0.5 mm for *T. parindicus* ($n = 15473$) and 58.9 ± 0.5 mm for *T. australiensis* ($n = 523$) (Fig. 2). The mean sizes at maturity are described by the equations

T. parindicus females:

$$y = \frac{1}{1 + e^{(-0.27\pm0.1)(\mathrm{CL}-52\pm0.5)}}, \quad r^2 = 0.99,$$

T. australiensis females:

$$y = \frac{1}{1 + e^{(-0.53\pm0.2)(\mathrm{CL}-58.9\pm0.5)}}, \quad r^2 = 0.98.$$

Cephalopod sexual maturity

The maximum recorded GSI values for the two *Uroteuthis* squid species were similar (up to 20%) and were approximately double those of each *Sepia* cuttlefish species (<10%) (Fig. 3). Our estimated size at 50% maturity showed variation among cephalopod species (Fig. 3). Of the two species of squid, *Uroteuthis* sp. 3 females matured at smaller size than *Uroteuthis* sp. 4. *Uroteuthis* sp. 3 as small as 80 mm and *Uroteuthis* sp. 4 as small as 100 mm had hydrated yellow eggs and GSI ≥5%. For cuttlefish, the largest growing species, *Sepia pharaonis* and *Sepia smithi*, mature at ≥106 and ≥90 mm, respectively. Both species however had a few individuals as small as 80 mm with GSI >2%. The most abundant species *Sepia elliptica* matures at ≥67 mm, which was similar to *Sepia papuensis* at ≥60 mm.

Spatial distribution and relative abundance

The commercial logbook catch of slipper lobsters was spread throughout the entire Gulf of Carpentaria fished area (Fig. 8). The mean retained catch rate was less than 15 kg day^{-1} in most regions, but there were localised areas where more than 30 kg day^{-1} was recorded. These were mostly in the south-eastern Gulf around Karumba and north of Mornington. Here, data from the fishery-independent prawn population monitoring surveys indicate that the

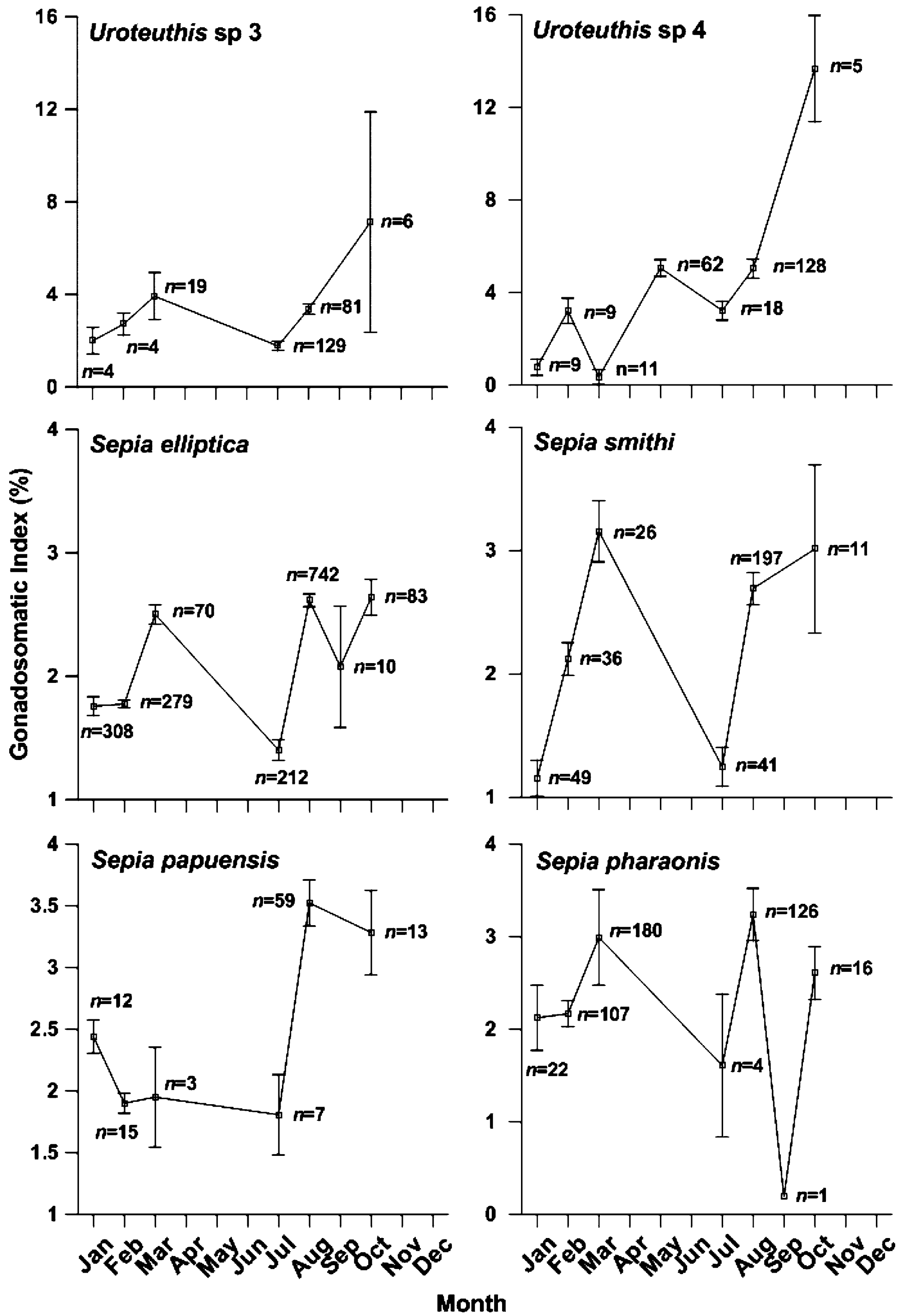

Fig. 5 Mean monthly female gonadosomatic index (%) of two species of squid and four species of cuttlefish caught in the Gulf of Carpentaria from August 2002 to July 2007

commercial catch is likely to be almost exclusively *T. parindicus*. The survey data showed that egg-bearing female slipper lobsters were caught in all regions. However, the proportion of both *Thenus* species that were egg-bearing varied, mostly between seasons rather than spatially (Fig. 8).

The spatial distribution of commercial squid catches was more restricted than those of slipper lobster (Fig. 9). Large catches over 250 kg day^{-1} were reported from several grids in the Vanderlins and Mornington Island regions. The fishery-independent survey data show that squid populations were in spawning condition throughout most of the year, with mature females representing a higher proportion during the dry season in most regions (Fig. 9).

The reported commercial catches of cuttlefish were almost exclusively from the southern and western parts of the Gulf of Carpentaria, particularly around the Vanderlins

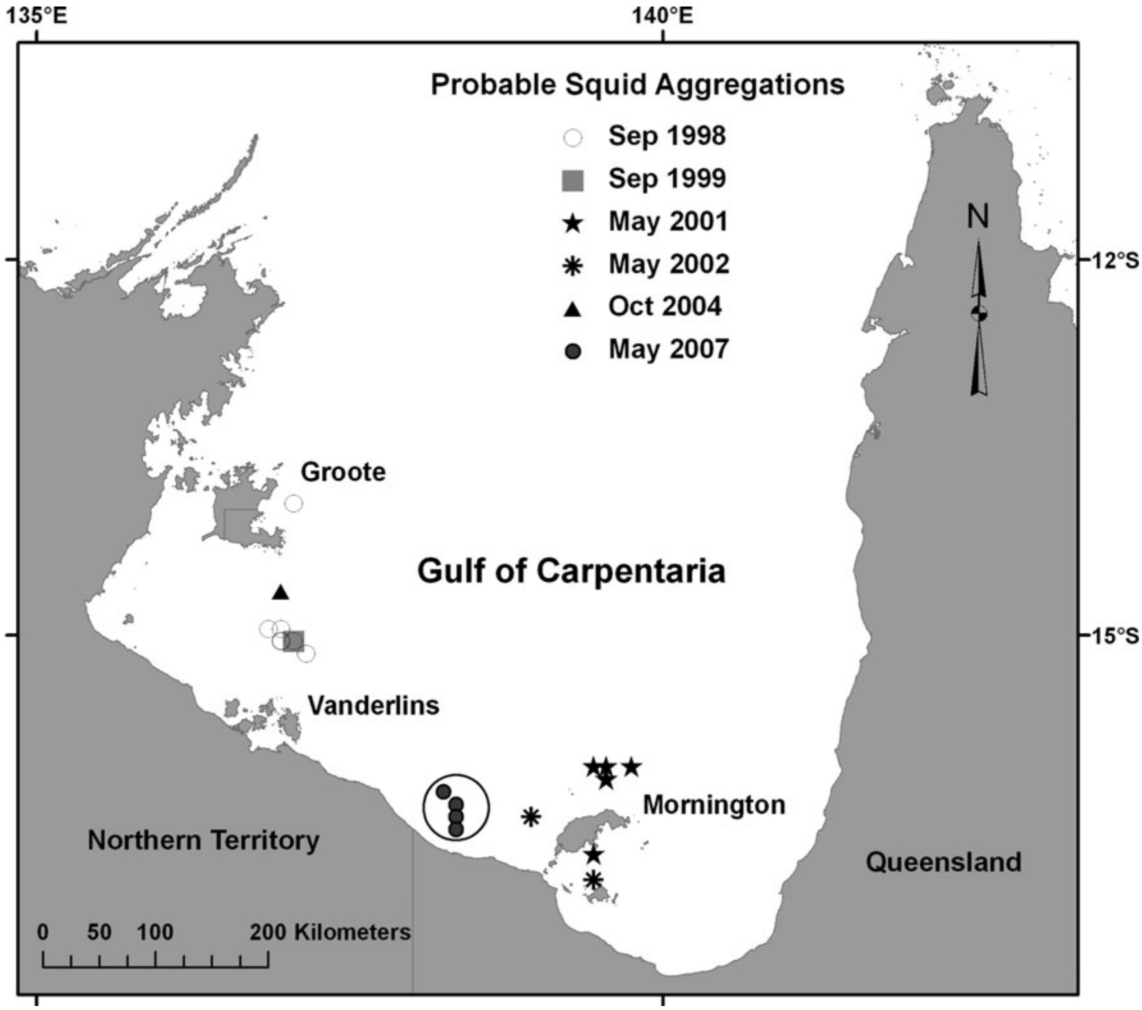

Fig. 6 Map of the Gulf of Carpentaria showing the location (*circled*) of the *Uroteuthis* sp. 4 spawning aggregation examined. Other probable squid aggregations (catches >400 kg vessel day^{-1}) in different years are also shown

Table 2 Biological data collected from the *Uroteuthis* sp. 4 spawning aggregation around Mornington Island on 23 May 2007

Sex	*n*	ML, range (mm)	ML, mean ± SE (mm)	BW, range (g)	BW, mean ± SE (g)	GSI, range (%)	GSI, mean ± SE (%)
Male	57	117–280	198 ± 5.9	27.5–142.2	74 ± 3.8	0.21–2.4	0.9 ± 0.06
Female	62	118–175	139 ± 1.7	28.8–87.2	48 ± 1.8	0.85–14.4	5.4 ± 0.4

ML mantle length, *BW* body weight

region (Fig. 10). The fishery-independent survey data indicated that cuttlefish spawning patterns varied among species, with a greater proportion of most species in spawning condition during the dry season (Fig. 10). This is particularly evident for the south Groote, Vanderlins, Mornington and Weipa regions. In contrast, a greater proportion of *S. elliptica* and *S. smithi* were in spawning condition during the wet season around Karumba (Fig. 10).

Discussion

The reproductive characteristics of byproduct species caught in the NPF varied widely. We found species-specific differences in size at maturity and temporal and spatial reproductive condition. The species examined spawned at regular intervals, with the populations spawning over an extended spawning season.

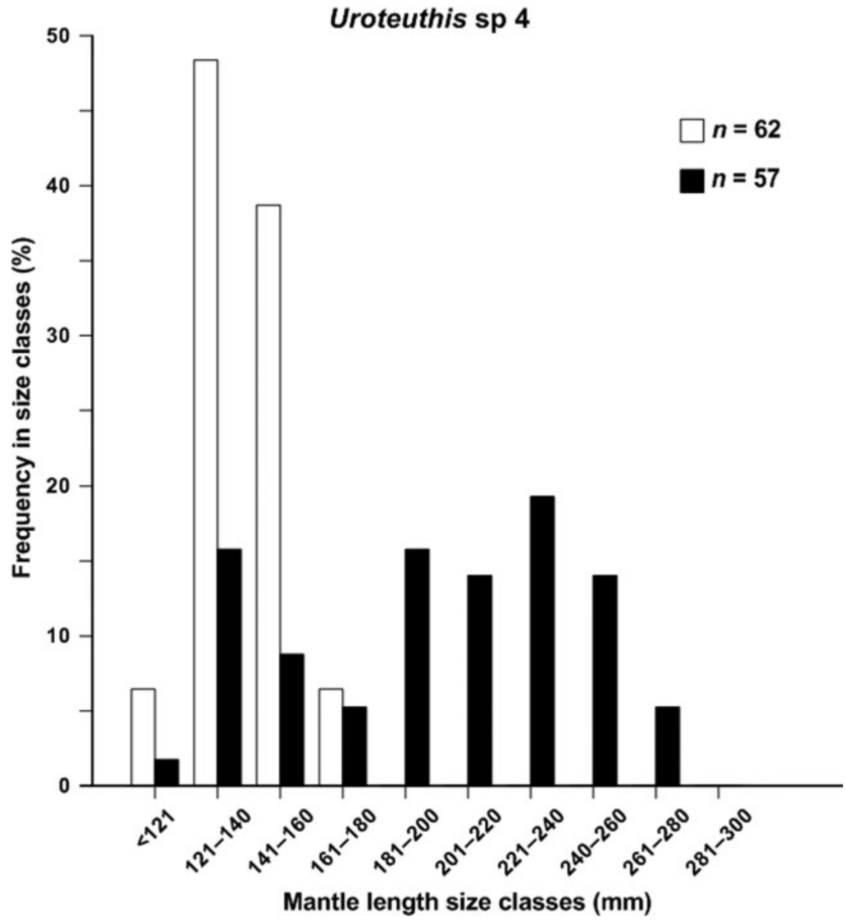

Fig. 7 Percentage length–frequency distributions of *Uroteuthis* sp. 4 caught from a single spawning aggregation (23 May 2007) west of Mornington Island (see Fig. 6). *White bars* females, *black bars* males

Slipper lobsters

The overall reproductive patterns appear to be similar for both species of lobster. *T. parindicus* mature at smaller size than *T. australiensis* and at a similar size to lobsters on the Queensland east coast [11]. According to Jones [11], both lobster species produce at least two egg masses per year, with peak recruitment of young adults to the fishing grounds in the wet season (January–March). A strong recruitment to the NPF during the wet season for both species has also been observed [15]. It appears that the majority of spawning activity occurs in the late dry season (August–October) in which the percentage of egg-bearing females increased from ~15% in July to over 40% in October (Fig. 4). It is unclear whether this spawning pulse extends into November and December, as samples were not collected during these months. For most months outside of the peak spawning period there was potential for some spawning activity for both species, as there was a small proportion of egg-bearing females present. This may be an adaptive response by these populations to reproduce under the variable environmental conditions that exist in tropical Australia, where rainfall patterns and nutrient inputs are highly seasonal; for example, other studies have found that large fluctuations in environmental factors such as temperature, salinity, wind and currents have the potential to influence the survival of larvae of other lobster species [16, 17].

Squid and cuttlefish

Reproduction in loliginid squids and sepiid cuttlefish is complex and encompasses a wide spectrum of behaviour and a large energy investment over an extended part of the short lifecycle [18]. There was variation in size at maturity for females for each of the six cephalopod species analysed. Of these species, size at maturity has been previously described for *Uroteuthis* sp. 4, *Uroteuthis* sp. 3, *Sepia pharaonis* and *Sepia elliptica*. Yeatman [14] estimated size at maturity for *Uroteuthis* sp. 4 and *Uroteuthis* sp. 3 to be 100 and 80 mm, respectively, which generally supports our findings. However, in the temperate waters of the Hawkesbury River (New South Wales, Australia), O'Donnell [19] found that *Uroteuthis* sp. 3 reached maturity around 100 mm, which is larger than our estimate of 87 mm. Higher water temperatures are likely to facilitate faster growth and smaller size at maturity for the northern individuals. Our size at maturity estimates for *Sepia*

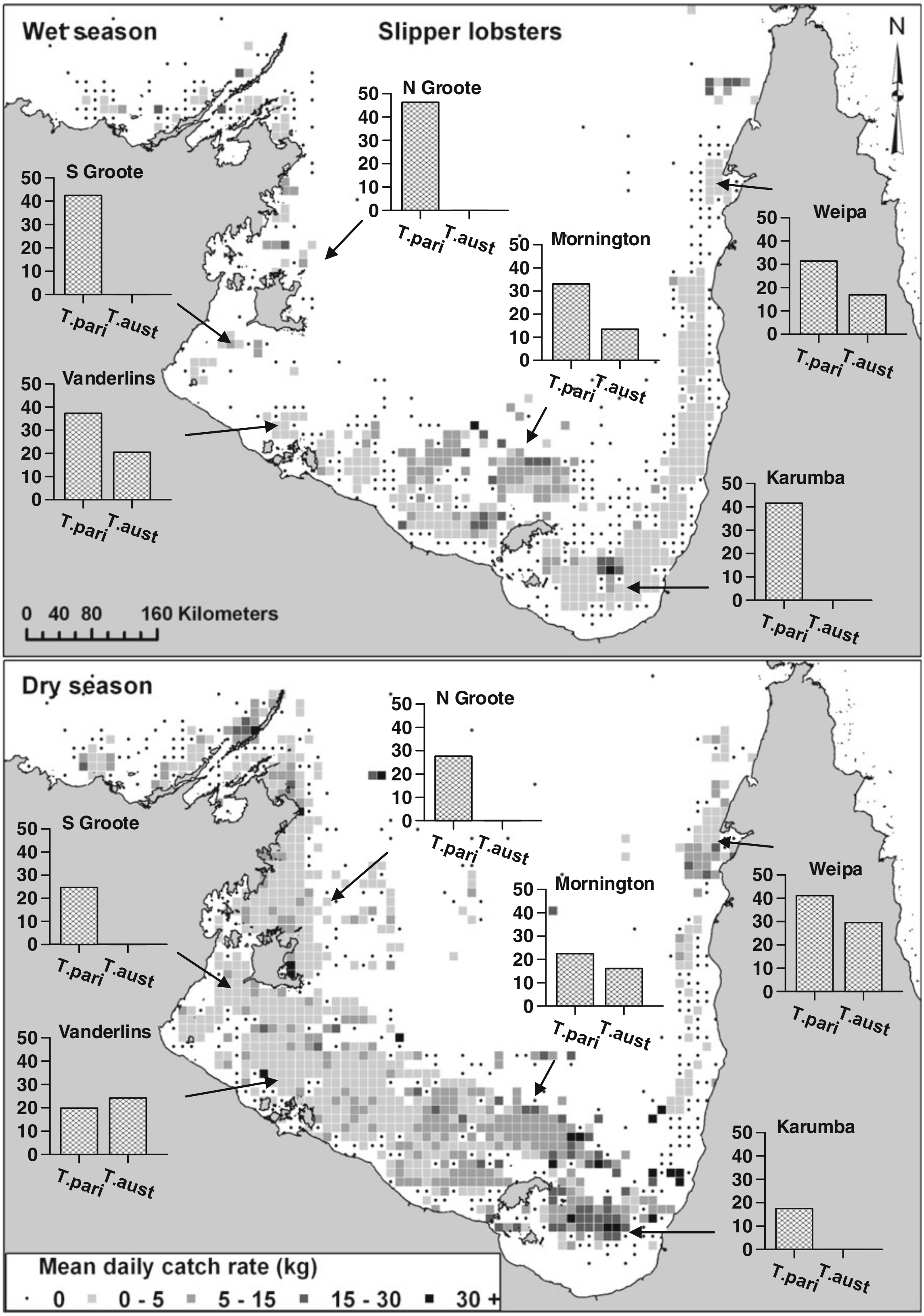

Fig. 8 Maps of the Gulf of Carpentaria showing mean daily commercial catch rates (*grid point*) of two species of slipper lobster (*Thenus*) for the wet (December–April) and dry (May–November) seasons (years 1998–2007). The percentage (histogram) of the adult female population that were egg-bearing (from fishery-independent survey data) for the wet (January–March) and dry (June–October) season are also shown. T.pari, *Thenus parindicus*; T.aust, *Thenus australiensis*

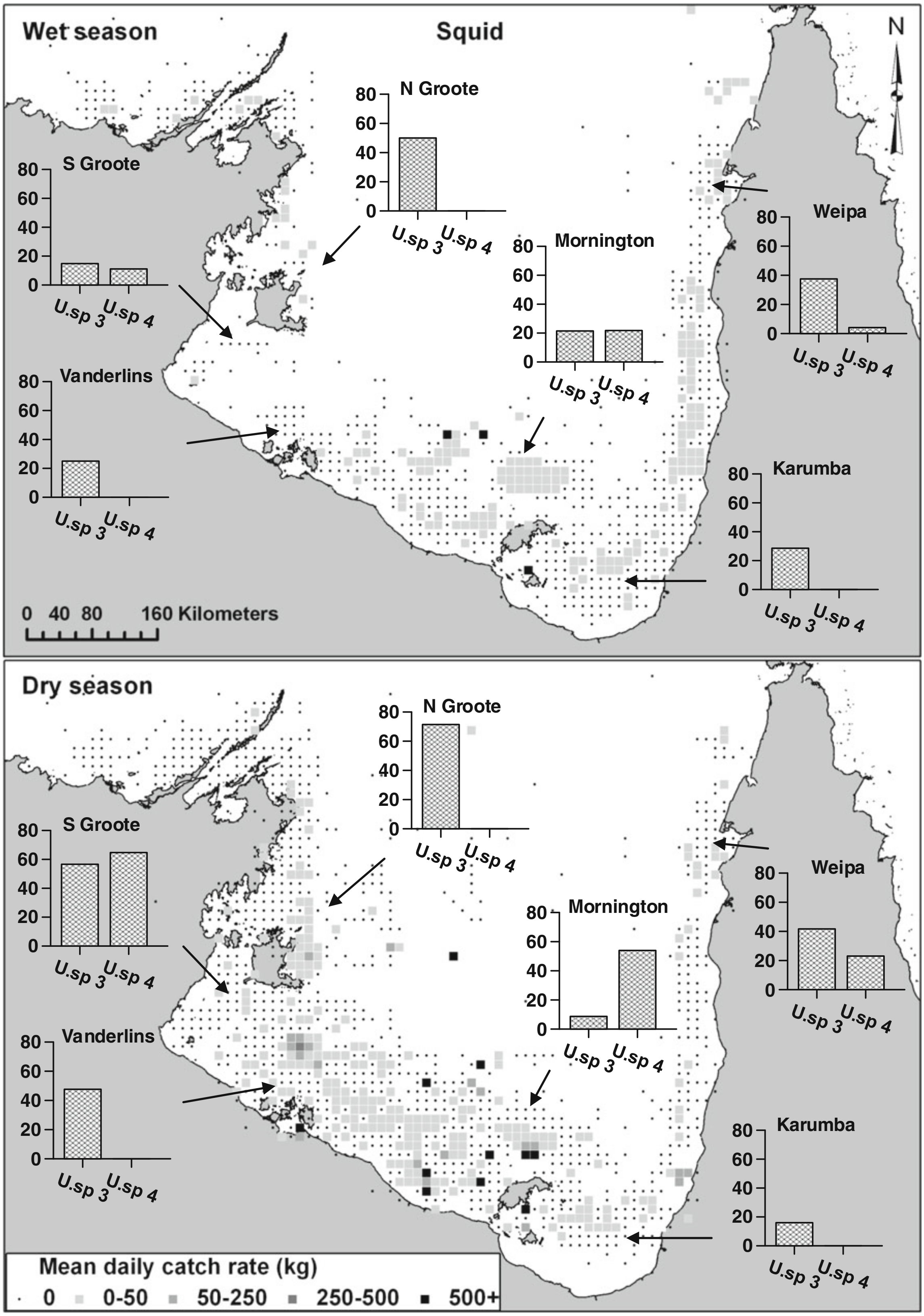

Fig. 9 Maps of the Gulf of Carpentaria showing the mean daily commercial catch rates (*grid point*) of two species of *Uroteuthis* squid for the wet (December–April) and dry (May–November) seasons (years 1998–2007). The percentage (histogram) of the adult female population in spawning condition (from fishery-independent survey data) for the wet (January–March) and dry (June–October) season are also shown. U.sp. 3, *Uroteuthis* sp. 3; U.sp. 4, *Uroteuthis* sp. 4

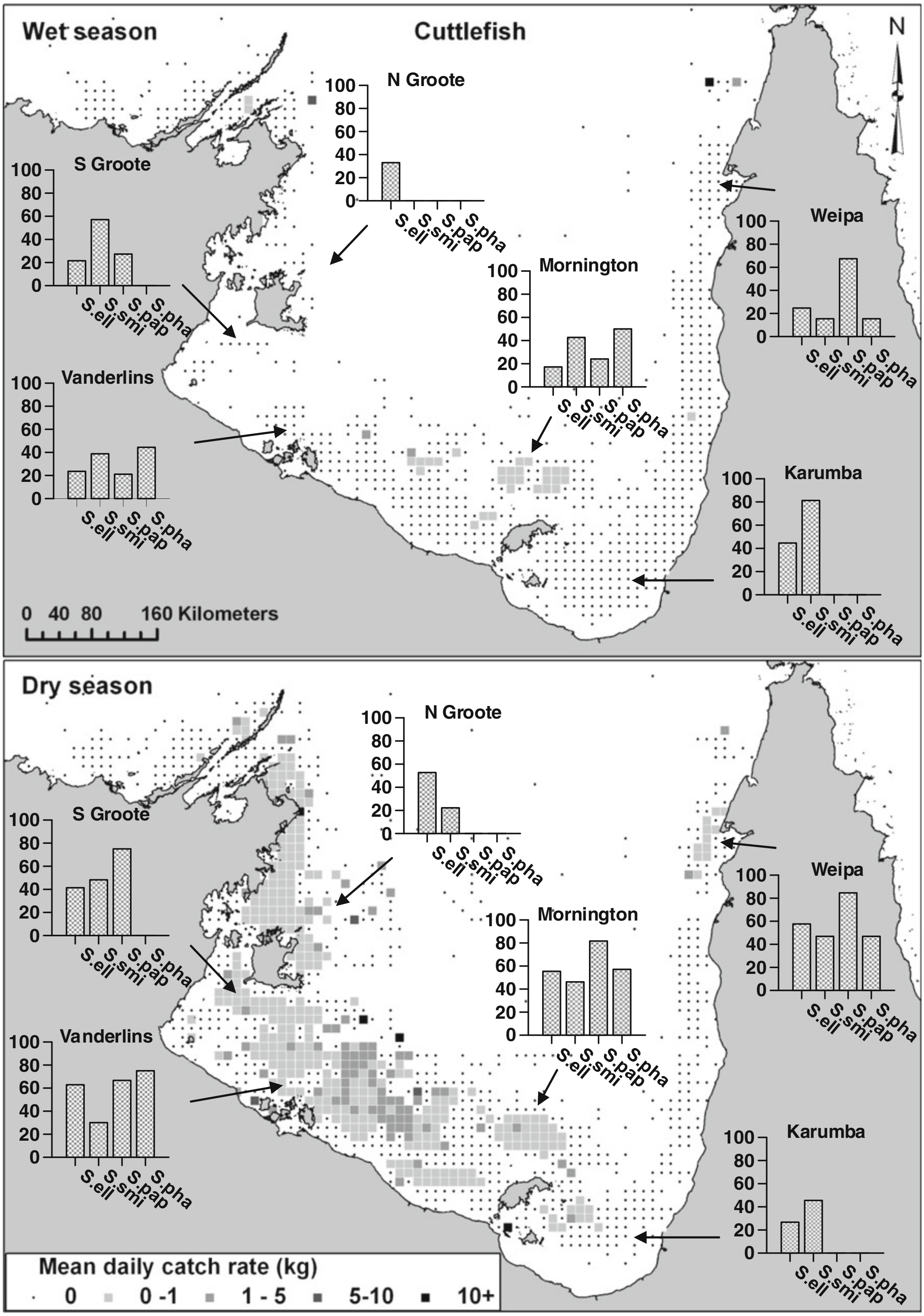

Fig. 10 Maps of the Gulf of Carpentaria showing the mean daily commercial catch rates (*grid point*) of four species of *Sepia* cuttlefish for the wet (December–April) and dry (May–November) seasons (years 1998–2007). The percentage (histogram) of the adult female population in spawning condition (from fishery-independent survey data) for the wet (January–March) and dry (June–October) season are also shown. S. ell, *Sepia elliptica*; S. smi, *Sepia smithi*; S. pap, *Sepia papuensis*; S. pha, *Sepia pharaonis*

pharaonis and *Sepia elliptica* were lower than other studies; for example, Gabr et al. [20] and Silas et al. [21] estimated size at maturity of *Sepia pharaonis* to be 122 mm (Suez Canal) and 120 mm (Madras coast), respectively, compared with our estimate of 106 mm for this species in Gulf of Carpentaria. Similarly, our size at maturity estimate of 67 mm for *S. elliptica* was slightly below the 75 mm determined by Silas et al. [21] (Madras coast) and Dunning et al. [22] (Gulf of Carpentaria). A marked plasticity has been noted in size at maturity for a number of cephalopods (*Loligo opalescens* [23], *Loligo pealei* [24], *Photololigo edulis* [25] and *Loligo vulgaris reynaudii* [26]). Factors such as size, age, food availability and environmental conditions including temperature and day length have been reported as possible explanations for these differences in size at maturity [25, 27, 28].

Interpretation of cephalopod dynamics on the basis of GSI should only be attempted with caution [29]. However, as an indicator of seasonality in maturity, GSI values largely confirmed interannual variability. The abundant inshore squid and cuttlefish species examined spawned throughout the year in northern Australia, with apparent seasonal peaks in egg production for some species. *Uroteuthis* sp. 3, *Uroteuthis* sp. 4, *S. smithi* and *S. papuensis* have an obvious peak in the late dry season (spring; September–October), which may suggest spawning at this time. In contrast, *S. elliptica* and *S. pharaonis* did not show clear seasonality in spawning. According to Jackson [30], Moltschaniwskyj and Doherty [31] and Sukramongkol et al. [32], other *Uroteuthis* species spawn in large aggregations throughout the year, with peaks in spring and autumn. The opportunistic sampling of a spawning aggregation in May 2007 (autumn) suggests that at least *Uroteuthis* sp. 4 does spawn at this time. Dunning et al. [33] also reported a spawning aggregation of *Uroteuthis* sp. 4 in August 1996 (late winter) north of the Vanderlin Islands. This spawning location was very similar to the probable spawning locations identified by the logbook catch records for September 1998, September 1999 and October 2004 (see Fig. 6). Another tropical squid, *Photololigo edulis*, also spawns in spring and autumn in the southern East China Sea [34]. The protracted spawning seasons of these species may be a strategy to compensate for variable environmental conditions that can affect hatching [35]. Similarly, Boletzky [36] found that the cuttlefish *Sepia officinalis* also showed protracted spawning in captivity over a period of 7 months. He also suggested that this spawning strategy is likely to be important under variable environmental conditions to counteract high mortality rates.

Management issues

Current regulation of catches of both *Thenus* species in the NPF is through a MLS and a prohibition on retaining egg-bearing females. Our estimate of maturity (CL_{50}) for *T. parindicus* of 52 mm CL is below the current MLS of 55 mm CL (~75 mm carapace width). As a result, a proportion of the mature females can spawn before they are vulnerable to fishing. As *T. parindicus* accounts for over 90% of the *Thenus* catch in the NPF [37], the current regulation should reduce the risk of recruitment overfishing. In contrast, our maturity estimate (CL_{50}) of 59 mm CL for *T. australiensis* is greater than the MLS, which is not protecting spawners. However the habitat preference for this species is likely to provide a level of protection, as they prefer coarser substrates and deeper water (>40 m) [11, 37]. The level of fishing effort in the NPF is higher in shallower water (<40 m) and on the finer particle substrates preferred by the targeted prawn species. However, if the *T. australiensis* population in the NPF was considered to be in decline or at risk, then a possible management option would be to increase the MLS to 80 mm CW for both species. The same recommendation was proposed for Queensland's East Coast Trawl Fishery [38] where *T. australiensis*, in contrast to the NPF, is the dominant *Thenus* species in catches [39]. This would increase egg production and reduce the likelihood of recruitment overfishing of *T. australiensis* [10].

Many species of cephalopods, including *Uroteuthis* sp. 3 and *Uroteuthis* sp. 4, aggregate when spawning [22]. This makes them potentially more vulnerable to targeted fishing. The targeting of squid aggregations by demersal trawling has the potential to disrupt mating behaviour [18] and also damage egg capsules attached to the seabed. Large spawning aggregations have been reported for other squid species, such as *Loligo vulgaris reynaudii* in South Africa [40], *L. pealei* off the US east coast [41] and for *L. opalescens* off California [42]. In contrast, cuttlefish are usually solitary except during spawning, where there may be localised small aggregations of mating pairs but not to the scale of squid aggregations [43]. The only reported exception to this is the large cuttlefish spawning aggregations of *Sepia apama* in southern Australia, where fishing closures are employed to protect the spawning stock [44]. We found no evidence of large spawning aggregations for any of the cuttlefish species examined. However, several commercial catches >10 kg day^{-1} have been reported in regions north and east of the Vanderlins, South Groote and south Mornington during the dry season (May–November). This may indicate some level of small aggregation for mating/spawning and should be investigated further to determine the reproductive characteristics of the species being caught. Information such as GSI, egg staging to determine egg maturity and sex ratio would be recommended.

Historical catches of cephalopods from Taiwanese trawlers in northern Australia indicate that the average annual catch of around 116 t of squid and 5 t of cuttlefish in the NPF from 1998 to 2005 is likely to be well below harvest capacity. In the late 1970s catches of squid were much greater than current NPF catches; for example, in 1978, there were 968 t of squid and 106 t of cuttlefish caught in the Gulf of Carpentaria by Taiwanese trawlers [45]. In the area northeast of Groote Eylandt alone, a total of ~48 t of squid were caught from 55 hauls [45]. These relatively large historical catches would most likely have little or no effect on current NPF squid stocks in the Gulf of Carpentaria unless the fishing operations significantly and irreversibly modified the benthic environment. Our understanding of the life history of tropical loliginid squids, while still limited, strongly suggests that they are fast growing, short lived (several months only), moderately fecund (a few thousand eggs produced), catastrophic spawners that recruit throughout the year, resulting in the presence of overlapping generations in all regions [28, 33, 46]. These characteristics suggest that recovery from heavy fishing pressure could be relatively rapid and not extend over several decades. Therefore, the current annual catch limit of squid before management action is required (500 t) is probably conservative. The fact that squid aggregations in the same locations within the NPF have been targeted at some level in multiple years without local depletion suggests a level of resilience at the current level of fishing. However, if this catch level is reached, then one management option might be to introduce a spatial or temporal closure to trawling of known squid spawning grounds, as has been implemented elsewhere [40, 47, 48].

The temporal closures (seasonal and diel) used to manage the targeted penaeid fisheries in the NPF may provide some level of protection, as squid catchability by benthic prawn trawls is known to be higher during daylight hours [22]. Loliginid squids have diel migrations where at night they move higher into the water column to feed and avoid predators [49]. Therefore, the daytime closure that is in place for the tiger prawn fishing season (August–December) in the Gulf of Carpentaria affords cephalopods some protection. The diel behaviour of spawning squid may also provide some level of protection during day fishing closures; for example, Downey et al. [50] observed spawning aggregations of *Loligo reynaudii* over several weeks and identified that squid generally aggregate at dawn and increase in numbers throughout the day before dispersing mostly at dusk. The identification of species-specific spawning aggregations in the NPF and understanding the dynamics of their diel spawning behaviour in relation to managed fishing practices is likely to be important. Furthermore, collection of samples from these aggregations by fishers or scientific observers to determine their biological characteristics should also be implemented by fishery management.

According to Jackson [46], tropical squid tolerate and even thrive in very warm conditions. Therefore, they are likely to be favoured by the predicted increase in seawater temperature in northern Australia due to climate change. Global warming is likely to increase growth rates and accelerate their brief life histories. Pecl and Jackson [51] predict that warmer temperatures will also lead to smaller eggs and smaller size at maturity. Thus, the overall effects of warming seas are difficult to predict. Should warmer waters lead to a higher turnover rate, squid may have the potential to become more of a targeted species rather than as byproduct in the future. As a result, more rigorous techniques to define stock size and dynamics may need to be considered. These may include traditional stock assessment methods such as those described by Pierce and Guerra [52], or newer techniques that combine hydroacoustic and minimum demersal survey swept area estimates of spawning biomass [53]. There has also been some recent success in estimating stock size from environmental conditions, particularly sea surface temperature [54, 55]. New risk assessment methods [56] that rely on evaluating the proportion of the cephalopod population being trawled by the NPF could also be investigated.

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