

Surviving under pressure and protection: a review of the biology, ecology and population status of the highly vulnerable grouper *Epinephelus daemeli*

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Abstract. *Epinephelus daemeli* is a threatened serranid grouper species that is restricted to the south-western Pacific Ocean, ranging from eastern Australia to northern New Zealand and the Kermadec Islands. Declines in its abundance due to fishing pressure were reported as early as 1916. Aspects of this species' biology and behaviour that make it vulnerable include its longevity, late age at maturity, protogynous hermaphroditism, territoriality and limited shallow reef habitat. Adults prefer complex habitat with caves and overhangs at depths of less than 50 m, whereas juveniles live in rock pools, shallow intertidal reefs and estuaries. *Epinephelus daemeli* lives at least 65 years and reaches 170-cm total length. Individuals change sex from female to male at ~100–110 cm and ~25 years. Absence of large (>100 cm) fish across a large part of their range has implications for reproduction. Although nearly fully protected, incidental bycatch still occurs. A lack of long-term data hinders determination of population status, but abundance appears to be much lower than before, except in remote regions (Kermadec Islands, Elizabeth and Middleton reefs) with extensive no-fishing areas. Further prohibitions on fishing in key locations are likely to be important for the recovery and long-term survival of this species.

Additional keywords: black cod, black rockcod, conservation, marine protected areas, otolith, Serranidae, spotted black grouper.

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Introduction

Fish species with K-selected life history characteristics (e.g. slow growth, late maturity, high longevity, large body size) are typically highly vulnerable to fishing mortality (Musick 1999; Reynolds *et al.* 2005; Abesamis *et al.* 2014). Depleted populations of such species are capable of recovering to carrying capacity levels following strong protection measures, particularly the implementation of 'no-take' marine protected areas (MPAs), but such recovery can take decades (Abesamis *et al.* 2014). The fish family Serranidae, commonly known as groupers and rockcods, includes some of the largest teleost fish in the oceans (Heemstra and Randall 1993). Large serranids appear to be particularly vulnerable to fishing because of their life history characteristics, aggregative spawning behaviour, strong site fidelity and protogynous sex-changing reproductive mode (Shapiro 1987; Huntsman and Schaaf 1994; Sadovy 1997; Sadovy and Eklund 1999; Abesamis *et al.* 2014). Not surprisingly, several large serranids are considered to be threatened and at risk of extinction (Sadovy de Mitcheson *et al.* 2013; IUCN

2014). Of the 87 species of *Epinephelus* currently recognised (Fishbase, <http://www.fishbase.org/home.htm>), seven are listed as critically endangered, endangered or vulnerable, with the others considered to be near threatened, least concern or data deficient (IUCN 2014).

One large *Epinephelus* species considered to be under threat is *E. daemeli* (Günther, 1876), which occurs in the south-western Pacific Ocean. It is commonly known as black cod or black rockcod in Australia, and spotted black grouper in New Zealand. The abundance of *E. daemeli* in eastern Australia has been substantially reduced by fishing over many decades. The species was previously considered to be common along the New South Wales (NSW) coast, and it was regularly sold through the Sydney fish markets (Marsh 2011). Declines in abundance were first observed in the early 1900s: 'At one time it [black cod] was fairly plentiful in the vicinity of Port Jackson [Sydney Harbour], but has become very scarce in recent years, owing to the havoc wrought by fishermen, and the increased shipping' (Roughley 1916). Because the species is considered to be excellent eating,

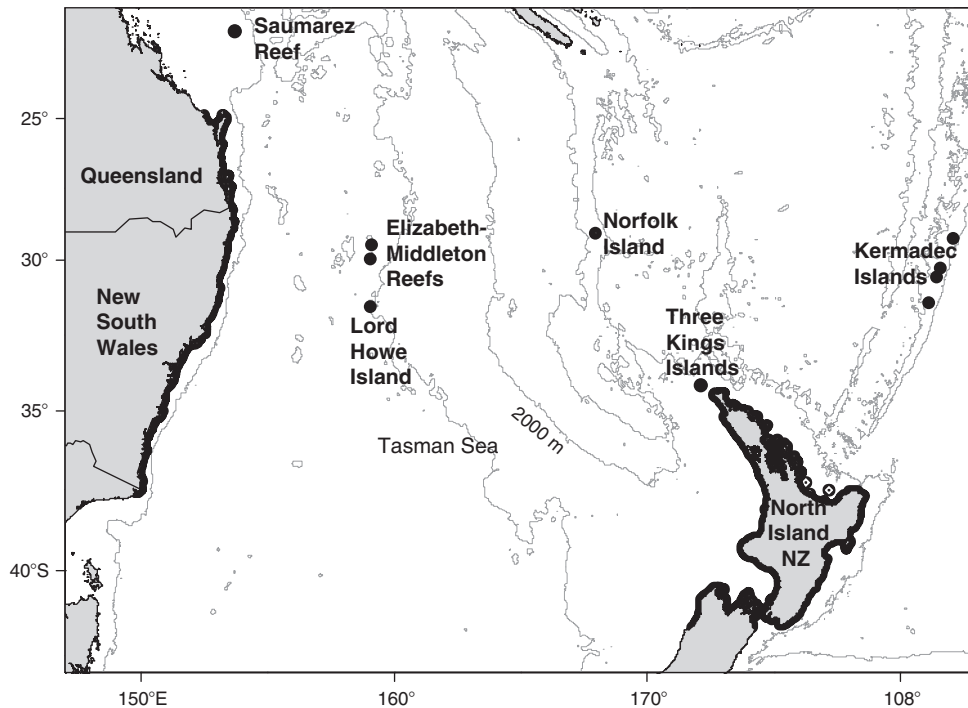


Fig. 1. Distribution of *Epinephelus daemeli* (bold line) in the south-western Pacific Ocean. *Epinephelus daemeli* ranges from eastern Australia in the west to northern New Zealand (NZ) and the Kermadec Islands in the east, including the subtropical islands and reefs of the northern Tasman Sea.

it was heavily targeted by fishers in the mid-20th century, particularly by spearfishers from the 1950s to the late 1970s (Young *et al.* 2015). Many articles in spearfishing magazines from this era, such as *Skindiving in Australia*, detailed the large numbers of adult *E. daemeli* taken. The species was considered a trophy fish by spearfishers, with the most popular fishing region being in northern NSW (Andrewartha and Kemp 1968). *Epinephelus daemeli* is easy to spear because of its occurrence in shallow habitat (see below) and its inquisitive nature (Lead-bitter 1992). In a single year (1976), NSW spearfishing competition records indicated that 137 *E. daemeli* were caught (Lincoln Smith *et al.* 1989). As a result of its declining abundance, the species became one of the first group of fish to be fully protected in NSW in 1983.

At Lord Howe Island (LHI), which is administratively part of NSW but lies 570 km east of the mainland NSW coast (Fig. 1), anecdotal information from local fishers indicates that *E. daemeli* was previously abundant and was heavily targeted there by recreational and commercial line fishing (for subsistence and local guesthouse supply) before its protection. Its status as a sought-after species before 1983 is supported by historical photographs from fishing competitions held in the 1970s (Fig. 2; Ian Hutton, LHI Museum, pers. comm.).

At Norfolk Island, fishers also targeted *E. daemeli* (Tofts 2006). Very large specimens were sometimes landed, although individuals >2 m illustrated by Tofts (2006) were probably *E. lanceolatus*. *Epinephelus daemeli* was protected at Norfolk Island, which is a self-governing territory in Australian Commonwealth waters, in 2012.

Off mainland New Zealand, *E. daemeli* is rare (see below) and it has rarely been targeted. However, it is vulnerable to incidental catch by recreational and commercial lining and, until it was protected throughout much of its range (in the Kermadec and Auckland Fisheries Management Areas) in 1986, was occasionally taken by spearfishers. The species is abundant at New Zealand's Kermadec Islands (Fig. 1). The remoteness of those islands (750–970 km from North Island, New Zealand) and the lack of harbours for sheltering mean that a commercial fishery never established there. Recreational fishing was limited to occasional passing yachts and a small number of New Zealand Government staff living on Raoul Island. Therefore, the Kermadec Islands population of *E. daemeli* was only lightly fished before the species was protected under fisheries legislation in 1986, and its habitat was protected by a 'no-take' marine reserve established in 1990.

Within Australia, *E. daemeli* is listed as a threatened species and classified as 'Vulnerable' under the Commonwealth Environment Protection and Biodiversity Conservation Act 1999 and the New South Wales Fisheries Management Act 1994. In New Zealand, it is classified as 'Not Threatened' by the Department of Conservation, but with the qualifiers 'Conservation Dependent' and 'Threatened Overseas' (Hitchmough *et al.* 2007). The first qualifier stems from the complete protection of *E. daemeli* in New Zealand waters since 1996, and the protection of its main New Zealand habitat at the Kermadec Islands by a 'no-take' marine reserve. The second qualifier refers to its Australian threatened species classification. The IUCN Red List classifies the species as 'Near threatened' globally based on past declines



Fig. 2. Some of the fish caught during a 1971 Lord Howe Island fishing competition. Approximately 15 serranid groupers (probably all *Epinephelus daemeli*) are visible hanging from the rack and lying on the ground. Other species include the carangid *Seriola lalandi* and lethrinids (probably *Lethrinus miniatus* and *L. nebulosus*). Photograph reproduced with permission of Lord Howe Island Museum.

and its naturally vulnerable life-history characteristics (Shuk Man and Ng 2006).

Despite legislative protection of *E. daemeli* across most of its geographic range, the species is subject to ongoing incidental fishing mortality and it has shown limited population recovery in areas from which it was depleted several decades ago. Concern about the population status of *E. daemeli* has led to several recent studies that have substantially increased our knowledge of its biology and ecology, although much of the information remains unpublished or is only available in scattered reports (Choat *et al.* 2006; Hobbs *et al.* 2008; Francis and Lyon 2012; Harasti and Malcolm 2013; Harasti *et al.* 2014). There is a need to review and consolidate the available information on *E. daemeli* to provide a foundation for further management measures and a basis for further research to fill the knowledge gaps. This paper provides a synthesis and review of published and unpublished studies of *E. daemeli* and presents new data, particularly in relation to its age and growth, as well as its size composition and abundance in NSW.

Results and discussion

External appearance and identification

Epinephelus daemeli is highly variable in colour, ranging from pale (almost white) to black, with irregular, often broken and indistinct, bifurcating, oblique dark bars on the body between the nape and caudal fin (Fig. 3; Randall and Heemstra 1991; Kuiter 2000; Francis 2012). Small, irregular, white spots may cover the body, and a key identifying feature is a black saddle on the top of the caudal peduncle. The pelvic, anal, second dorsal and caudal fins have a narrow white margin and a submarginal black band, although these are not always visible in large or dark individuals. There are distinct canine teeth in both the upper and lower jaws. Variation in colour among individuals appears to be

primarily habitat related, because dark animals are generally seen in caves and pale animals are found over sand, rocky reefs or swimming in midwater (D. Harasti and H. Malcolm, pers. obs.). Individuals seen in the open but lying in small undulations in rocky reef habitat are often cryptically coloured, with a dark background colour and white blotches. Fish can change colour in seconds from black to white with dark bars or almost completely pale, and vice versa (Ayling and Cox 1982; M. Francis, D. Harasti and H. Malcolm, pers. obs.). Rapid colour changes have been observed during interactions among individuals (e.g. two fish circling each other with fins erect).

Smaller *E. daemeli* may be confused in appearance with other groupers, such as the estuary cod (*E. coioides*) and camouflage cod (*E. polyphkadion*), particularly in Queensland waters. Larger adults could be confused with bar cod (*E. ergastularius*) and the giant or Queensland grouper (*E. lanceolatus*). In addition, the Indo-Pacific deep-water grouper *E. octofasciatus*, which is increasingly being caught using power winches in the south-western Pacific, may be misidentified as *E. daemeli*.

Distribution

Epinephelus daemeli is a south-western Pacific Ocean endemic species (Fig. 1). It ranges from the east coast of Australia, through the subtropical islands and reefs of the Tasman Sea (LHI, Elizabeth and Middleton reefs and Norfolk Island) to the Kermadec Islands and northern New Zealand (Randall and Heemstra 1991; Francis 1993; Heemstra and Randall 1993). It is most abundant in the latitudinal range ~28–35°S. In Australia, its range extends from southern Queensland to eastern Victoria, but it is not known from Tasmania (Heemstra and Randall 1993; Pogonoski *et al.* 2002; Hobbs and Feary 2007; Harasti and Malcolm 2013). The main distribution of the species on the Australian mainland coast is in NSW, with adults occurring

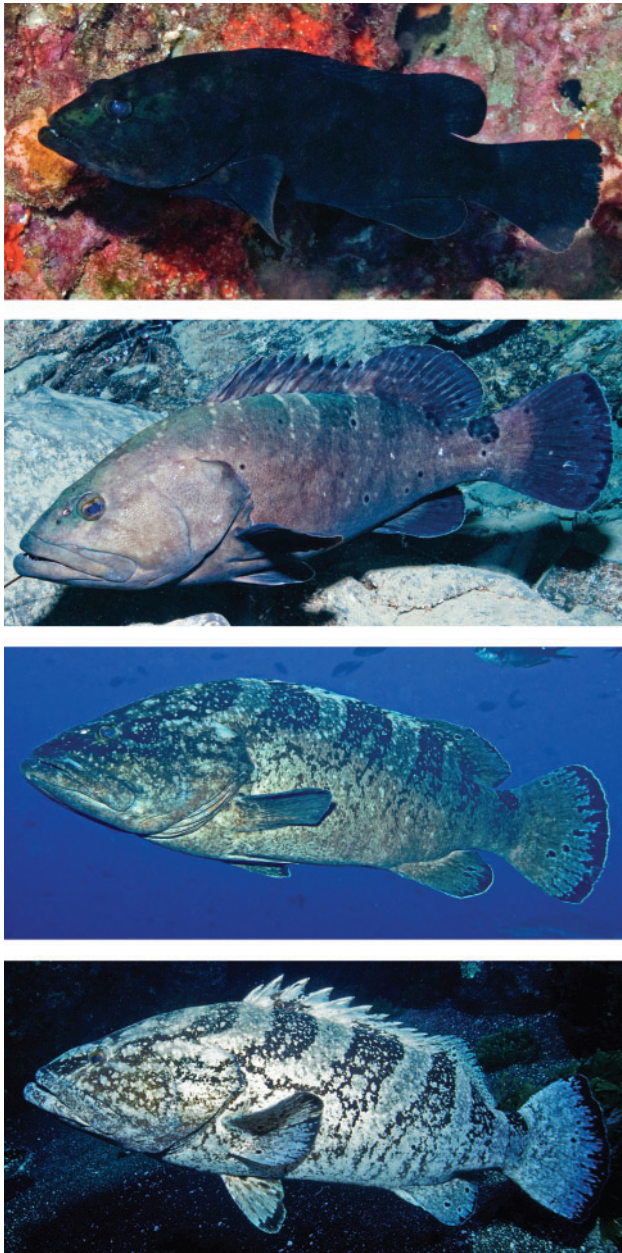


Fig. 3. Variations in colour pattern in *Epinephelus daemeli*.

primarily north of Sydney ($\sim 34^{\circ}\text{S}$; Harasti and Malcolm 2013) and juveniles from Port Stephens (32.7°S) south to Ulladulla (35.4°S ; Harasti *et al.* 2014). The northern limit of its distribution in Australia is uncertain, but it apparently reaches at least Bundaberg (24.9°S) on the mainland, the northern end of Fraser Island (24.5°S) and further offshore at Saumarez Reef (21.8°S , 153.7°E ; Johnson 1999; M. McGrouther, Australian Museum, pers. comm.; J. Johnson, Queensland Museum, pers. comm.). Records from further north than that may have been other misidentified species of *Epinephelus*. In the south, the species is rarely recorded from Victoria (a juvenile of 212-mm standard length from the Genoa River, Mallacoota, is held at Museum

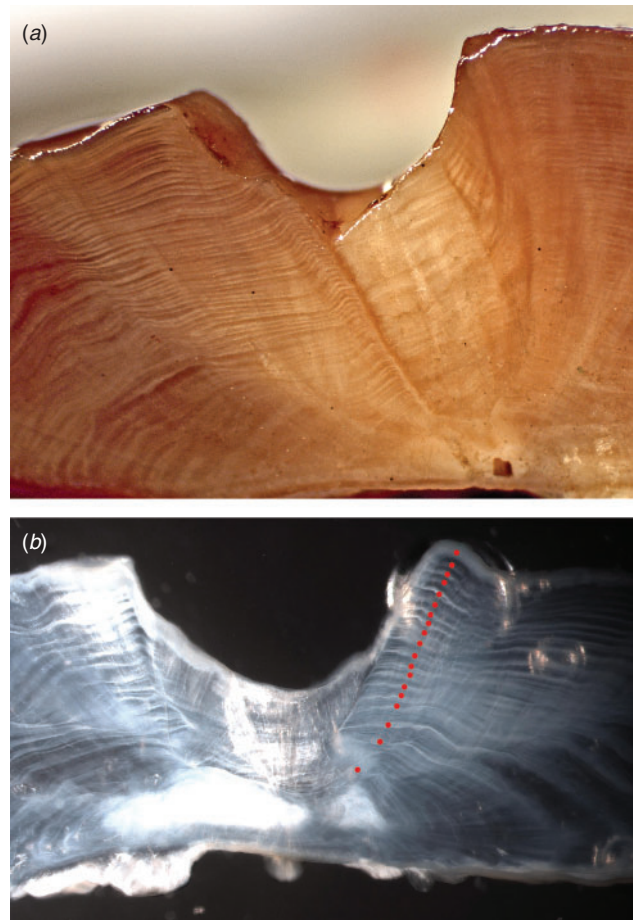


Fig. 4. (a) Sectioned otolith from a 119 cm male *Epinephelus daemeli* from Raoul Island, Kermadec Islands (estimated age 56 years). (b) X-Ray of an otolith section from a 91-cm fish from Solitary Islands, New South Wales (estimated age 19 years).

Victoria). A specimen reported from Kangaroo Island in South Australia (Randall and Heemstra 1991; Heemstra and Randall 1993; SAMA F5430 in the South Australian Museum) differs from *E. daemeli* in several anatomical features (including the number of soft dorsal fin rays and lateral line scales) and its true identity is unknown (Gomon *et al.* 2008; M. Gomon, Museum Victoria, pers. comm.).

In New Zealand, *E. daemeli* is found primarily around the north-eastern North Island and at the Three Kings Islands (Hardy *et al.* 1987; Paulin and Roberts 1992; Francis 1996b, 2012; Brook 2002; C. Worthington, pers. comm.). It has been recorded as far south as Cook Strait (41.5°S) and Westport (41.7°S), but is rare south of Cape Brett (35.2°S). Breeding is unlikely to occur in mainland New Zealand waters and individuals occurring there are probably vagrants from upstream sources, such as Norfolk Island and LHI.

At the Kermadec Islands, *E. daemeli* is occasional or common throughout the island chain (Francis *et al.* 1987), with many over 1 m in length being observed under ledges and near boulders from shallow water ($\sim 3\text{-m}$ depth; Schiel *et al.* 1986) down to over 25 m (M. Francis, unpubl. obs.).

Stock structure

Preliminary research based on small sample sizes found little genetic differentiation between *E. daemeli* from Elizabeth and Middleton reefs and coastal NSW, but larger samples and testing of more loci are required to confirm this (Appleyard and Ward 2007; van Herwerden *et al.* 2009; Marsh 2011). Given its geographic proximity to Elizabeth and Middleton reefs, LHI *E. daemeli* are likely to form part of the same stock. The stock relationships of fish from Norfolk Island, the Kermadec Islands and northern New Zealand are unknown. No tagging studies have been undertaken to determine the scale of movements in this species.

Habitat

Juveniles

Post-larval and juvenile *E. daemeli* (<30-cm total length (TL)) occur mainly in rock pools and shallow rocky intertidal areas (Paulin and Roberts 1992; Lardner *et al.* 1993; Griffiths 2003; Harasti *et al.* 2014). They have also been found on mussel farm ropes in north-eastern New Zealand. A recent study along the NSW coast found juveniles in rock pool habitats that were boulder and/or overhang dominated, but not algal dominated (Harasti *et al.* 2014). Fish in these intertidal habitats measured 3–26 cm TL and they were observed to tolerate a wide range of water quality parameters, particularly temperature. They also exhibited strong site fidelity, with individuals occurring in the same rock pool for up to 471 days. Although juvenile *E. daemeli* were not found in shallow intertidal habitats of northern NSW by Harasti *et al.* (2014), recent diving and baited remote underwater video (BRUV) surveys have found juveniles (10–30 cm) on rocky reef habitat within estuaries in northern NSW, adjacent to the Solitary Islands (H. Malcolm, unpubl. data). At Elizabeth and Middleton reefs, juveniles (25–30 cm TL) were very cryptic, because they were only found hiding among crevices and overhangs of the reef complex (Choat *et al.* 2006).

In NSW, juvenile *E. daemeli* are more common along the central to southern coast (~32–35°S) than in northern NSW (~28–31°S; Harasti *et al.* 2014). This is likely a result of larval dispersal by the East Australian Current (EAC), a western boundary current with jets and eddies that can transport larvae southwards from northern NSW (Booth *et al.* 2007). However, north-to-south coastal connectivity and successful recruitment are likely to be highly variable at a range of temporal scales, because the EAC often separates from the Australian mainland coast around Smoky Cape (~31°S; Syahailatua *et al.* 2011; Cetina-Heredia *et al.* 2014).

Subadults

Subadults are defined here as fish of 30–70 cm TL. In NSW, subadult *E. daemeli* have been observed in estuaries, particularly along rocky breakwalls, and on coastal rocky reefs. Subadults have a large range across the state in these habitats (Harasti and Malcolm 2013). For example, along the southern NSW coast *E. daemeli* are regularly sighted in Wagonga Inlet, Narooma (~36°S). At LHI, subadults are found on carbonate reef within the lagoon and on reefs around the Admiralty Islands. Subadults were also recorded at Elizabeth and Middleton reefs associated with coral reef habitat and they were

generally observed in the open (Choat *et al.* 2006; Hobbs and Feary 2007; Pratchett *et al.* 2011).

In mainland New Zealand, the greatest numbers of subadults occur from Cape Reinga to Cape Karikari (Brook 2002; C. Worthington, pers. comm.). They occur throughout Pāren-garenga Harbour, particularly in broken sandstone habitat (Hayward *et al.* 2001). Abundance drops between Cape Karikari and Cape Brett, but they are often found in areas with good oceanic water flow that are not too exposed to easterly storms, for example Stephenson's Island, Cavalli Islands, inner Bay of Islands and sheltered shores near Cape Brett. In offshore island sites (e.g. Poor Knights Islands), subadult and adult *E. daemeli* are usually seen shallower than 20 m sheltering in caves and crevices (Doak 1972; Ayling and Cox 1982).

Adults

Adult *E. daemeli* predominantly occur at depths <50 m and prefer depths shallower than 25 m (Francis 2012), but they have been recorded occasionally from deeper water (Marsh 2011; New South Wales Department of Primary Industries 2012). Queensland Museum specimens of *E. daemeli* from southern Queensland, near the northern limit of its range, were reportedly caught in depths of 100–200 m (J. Johnson, pers. comm.). A large fish, estimated at ~1.8 m TL, was caught at a depth of 300 m at LHI and other *E. daemeli* have been reported from there in depths >100 m (K. Galloway, pers. comm.). A 70-kg fish was reported from 110-m depth by an observer on a boat carrying out exploratory fishing north-west of Macauley Island at the Kermadec Islands in September 1992 (New Zealand Ministry for Primary Industries (MPI), unpubl. data). However, some of these reports may have been of misidentified *E. octofasciatus*.

Adults generally inhabit coastal rocky reefs and offshore coral reefs. On rocky reefs, they are commonly associated with complex topography around islands and emergent rocks. In coastal waters, *E. daemeli* are found in or near rock caves and gutters, overhangs, boulders, corals and on open reefs. Overhangs and caves, in particular, are important for this species, which may occupy the same cave for decades (Doak 1972; Ayling and Cox 1982; Heemstra and Randall 1993; Pogonoski *et al.* 2002; New South Wales Department of Primary Industries 2012). During visual surveys in NSW, many *E. daemeli* were initially observed in the open but then swam to more complex structures (e.g. overhangs) for shelter or swam away rapidly. Up to 60% of fish recorded in visual surveys were considered to be cryptic because they were hidden from immediate view (Harasti and Malcolm 2013).

At some tropical oceanic locations (e.g. Elizabeth and Middleton reefs), coral reef habitats support relatively high densities of *E. daemeli* (Choat *et al.* 2006; Hobbs and Feary 2007; Pratchett *et al.* 2011). Thus, *E. daemeli* are able to persist and presumably complete their life cycle in very contrasting habitats (rocky reefs and coral reefs) and environments.

At Elizabeth and Middleton reefs, *E. daemeli* are uncommon in areas exposed to heavy wave action (Choat *et al.* 2006), but they are abundant at the Kermadec Islands where there is little sheltered habitat. In mainland Australia, they appear to prefer reefs exposed to current (Harasti and Malcolm 2013). For example, during an underwater survey, 10 adult *E. daemeli*

Table 1. Details of samples of *Epinephelus daemeli* aged using otolith bands

Date	Number of fish	Age (years)	Total length (cm)	Location	Source
1975–76	Multiple	5–6	59.5	New South Wales, Australia	D. Francois (pers. comm.)
1985–87	10	31–65	106–156	Raoul Island, Kermadec Islands	M. Francis (unpubl. data)
April 2011	1	17	80.5	New South Wales, Australia	Harasti and Malcolm 2013
May 2011	1	42	127	Lord Howe Island	D. Harasti (unpubl. data)
2011–14	6	1–19	15–91	New South Wales, Australia	D. Harasti (unpubl. data)
June 2015	1	42	155	New South Wales, Australia	H. Malcolm (unpubl. data)
July 2015	1	52	147	Queensland, Australia	J. McGilvray (unpubl. data)

were recorded at the northern end of South Solitary Island, NSW, which has complex habitat (canyons, caves and boulders) and is subject to strong currents, yet only one was recorded near the north-western corner of North Solitary Island, an area with similar habitat but no current. Around the corner from the latter, at the northern end of North Solitary Island, which is often subject to strong current, eight adults were recorded (Harasti and Malcolm 2013). It appears that adult *E. daemeli* are less active during periods of lower temperatures, when they are more likely to be found residing in caves (Harasti and Malcolm 2013).

At LHI, adult *E. daemeli* have also been detected using BRUVs on low-relief sea floor with minimal, small patch reefs (Neilson *et al.* 2010). These fish were very inquisitive and attempted to feed aggressively on the BRUV bait. At the Kermadec Islands, adults are similarly inquisitive and investigate divers closely (M. Francis, pers. obs.). This behaviour makes it difficult to define their preferred habitat because they may be attracted to diver activity from tens or even hundreds of metres away. Large adults were found in the open at Elizabeth and Middleton reefs, particularly within lagoons (Leadbitter 1992; Choat *et al.* 2006). We hypothesise that *E. daemeli* territories are centred on caves or near overhangs, but that they frequently range over rocky reef and adjacent low-relief seabed in search of food or mates, and perhaps in defence of their territorial boundaries.

Size

The maximum length of *E. daemeli* is unclear, because few large fish have been measured. Francis (1988, 1996a) estimated that Kermadec Islands fish reach 200 cm TL, but subsequently revised this down to 170 cm (Francis 2012). Although very large fish do occur at the Kermadecs and a length of 200 cm is plausible, this has not been verified from actual measurements. Paulin and Roberts (1992) reported the maximum length in New Zealand as 180 cm. At LHI, the species is reputed to reach at least 180 cm TL and weigh over 100 kg (K. Galloway, pers. comm.). At Elizabeth and Middleton reefs, *E. daemeli* estimated at up to 140 cm long were recorded during underwater transect surveys (Choat *et al.* 2006). Off mainland Australia, *E. daemeli* reaches at least 155 cm TL and 81.6 kg weight (Hutchins and Swainston 1986; Table 1). The largest fish accurately measured from calibrated stereovideo (Harvey *et al.* 2004) during diver surveys and baited video surveys over the past 5 years was 140 cm TL (New South Wales Department of Primary Industries, unpubl. data).

During 2011, an underwater visual survey at the relatively pristine Kermadec Islands Marine Reserve observed 45

E. daemeli. They ranged in estimated length from 30 to 130 cm TL, with a mean of 99 cm TL (C. Duffy, New Zealand Department of Conservation, unpubl. data).

Growth

No studies have been published on the growth rate or longevity of *E. daemeli*, but it has been widely assumed to be a slow-growing species, as is typical of groupers of this size. However, unpublished age data from several small samples of *E. daemeli* are available (Table 1) and are reported below. The age estimates and our analyses are considered tentative because: (1) otoliths were aged by several different readers and there was no comparison of age estimates among readers; (2) otolith ageing has not been validated in this species; (3) specimens came from multiple scattered locations over an extended time period; and (4) the sample size was small. Nevertheless, in the absence of better information, we use these age estimates to derive preliminary estimates of longevity, growth rate and ages at sexual maturity and sex change. Support for these analyses comes from the fact that otolith growth bands are distinct and easily counted (Fig. 4), and similar otolith bands have been validated as annual by marginal increment analysis, oxytetracycline injection or bomb radiocarbon dating in at least six other species of *Epinephelus* (Bullock *et al.* 1992; Manickchand-Heileman and Phillip 2000; Wyanski *et al.* 2000; Grandcourt *et al.* 2005; Fennessy 2006; Reñones *et al.* 2007; Lombardi-Carlson *et al.* 2008; Cook *et al.* 2009; Costa *et al.* 2012; Conдини *et al.* 2014).

Ten *E. daemeli* collected from the Kermadec Islands in 1985–87 were aged using burnt half-otoliths viewed under reflected white light. Age estimates ranged from 31 to 65 years (Table 1). Only the head was available for the oldest animal, so it could not be measured or sexed. The head measured 38 cm from the snout to the severed end of the backbone (assumed to be near the back of the skull) and 45 cm from the snout to the cut edge on the ventral side (assumed to be the isthmus). Total length was estimated from these measurements using body proportions measured on a lateral underwater photograph of a large, live *E. daemeli*; the estimates were 154 cm using the backbone measurement, and 156 and 168 cm for the isthmus measurement (for two possible extreme locations where the cut was made). A fourth total length estimate, based on the fisher's estimate of 'three and a half feet' for the length of the trunk (=107 cm), was 157 cm. After discarding the larger of the two isthmus estimates, the mean of the three remaining length estimates was 156 cm. The estimated weight of this fish (30 kg) seems to be too low for a fish of this size.

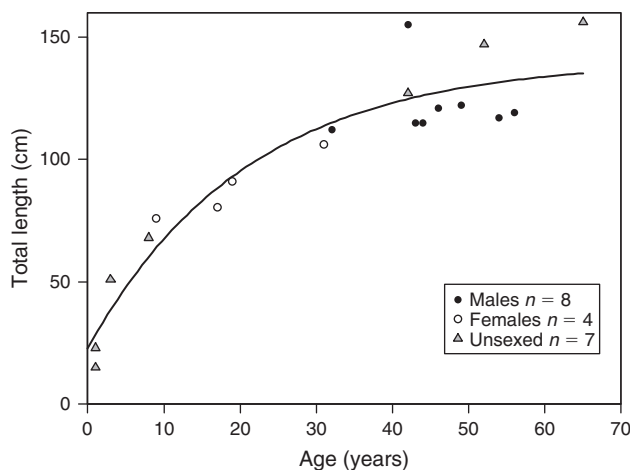


Fig. 5. Length-at-age data for *Epinephelus daemeli* from Kermadec Islands, mainland New South Wales and Lord Howe Island (see Table 1 for details) with a fitted Von Bertalanffy growth curve. The oldest fish (~65 years) was not measured and is plotted at an estimated length of 156 cm (see text for details).

An unmeasured 70-kg *E. daemeli* from Norfolk Island was estimated to be ~58 years old based on otolith band counts (Clifton 2001). Ten other fish from LHI and mainland NSW and Queensland (Table 1) have also been aged from otoliths.

The available length-at-age data are plotted in Fig. 5. The greatest estimated age was 65 years for the unmeasured fish that was thought to be ~156 cm TL. A von Bertalanffy growth curve was fitted to the length-at-age data using R package FSA (version 0.1.7, <https://www.rforge.net/FSA/Installation.html>, accessed 11 July 2015), which fits non-linear curves using R package nlstools. The growth model was:

$$L_t = L_\infty \left[1 - e^{-K(t-t_0)} \right]$$

where L_t is the expected length (cm) at age t years, L_∞ is the asymptotic maximum length (cm), K is the Brody growth coefficient (year^{-1}), t is the age (years) and t_0 is the theoretical age at zero length (years).

Estimated parameters for the growth curve (with 95% confidence intervals) were: $L_\infty = 140.4$ cm (116.0, 164.9), $K = 0.0478$ year^{-1} (0.0146, 0.0811) and $t_0 = -3.71$ years (-8.74, 1.31). The growth curve fitted the data for younger fish (up to 32 years old) well, but there was considerable variability in length-at-age among older fish. The high intercept of the growth curve on the y-axis suggests that either the ages of the young fish (and potentially all fish) were underestimated or that only larger individuals of the younger age classes were sampled. The latter scenario is highly plausible given the cryptic behaviour and habitat of small juveniles. Alternatively, it may reflect the small sample size, as t_0 was poorly estimated (but its confidence intervals nevertheless included zero years).

Clearly more samples are required to better define the growth curve and to investigate whether there is any regional variation in growth rate. Obtaining further otolith samples from *E. daemeli* in regions where it is protected is problematic. However, non-lethal ageing of other vulnerable serranids has

been accomplished using dorsal fin spines (Murie *et al.* 2009; Hobbs *et al.* 2014) and that approach warrants investigation for *E. daemeli*.

Nevertheless, we tentatively conclude that growth is relatively rapid in the first 10 years, by which time fish have grown to ~67 cm TL, but then declines so that fish reach ~95 cm TL at 20 years of age. Beyond that, growth slows considerably, but may be variable. Very large *E. daemeli* have yet to be measured and aged, so longevity is likely to be greater than 65 years. Based on a maximum age of 65 years, the instantaneous mortality rate M was estimated to be 0.07 using the Hoenig regression method (Hoenig 1983).

The maximum estimated age of *E. daemeli* (~65 years) is not surprising because other large *Epinephelus* species reach comparable or greater ages: *E. niveatus* lives to at least 54 years, *E. caninus* to 55 years, *E. marginatus* to 61 years and *E. flavolimbatus* to 85 years (Morales-Nin *et al.* 2005; Reñones *et al.* 2007; Cook *et al.* 2009; Costa *et al.* 2012).

Reproduction

Serranid groupers are protogynous sex changers, with many fish beginning life as females and later changing into males (Shapiro 1987; Heemstra and Randall 1993). However, primary males and large, old females have been reported in some species, and social cues such as population density can alter population sex ratios in experimental situations (Reñones *et al.* 2010; Liu and Sadovy de Mitcheson 2011; Costa *et al.* 2012), indicating that sex determination is complex in at least some species. As yet, there is no evidence of primary males or old females occurring in *E. daemeli*.

The largest female in our aged sample was 106 cm TL and the smallest male was 112 cm TL (Fig. 5), so there was no overlap between the sexes. However, this may be an artefact of the small sample size, which is inadequate for accurate estimation of the length at sex change. Francis (1988) used a subset of these data from the Kermadec Islands to estimate that sex change occurs in the length range 100–110 cm TL, an estimate that has been repeated by subsequent authors (Paulin and Roberts 1992; Heemstra and Randall 1993; Francis 1996a, 2012). The larger dataset now available (Fig. 5) does not permit any refinement of that estimate because no additional fish have been sampled over the relevant length range. If our growth curve is reliable in this range, sex change occurs at ~22–28 years of age, with our best estimate being ~25 years.

Seventeen fish examined from Sydney spearfishing competitions in the mid-1970s were immature at standard lengths of 30–50 cm (~35–60 cm TL; D. A. Pollard, unpubl. data; in a 1981 letter from D. D. Francois, Director of NSW State Fisheries). An ~69-cm TL fish caught near Wellington, New Zealand, was an immature female and a 77.5-cm fish from Middleton Reef had no apparent gonads (Whitley 1937), suggesting it was immature. Given the estimated length at sex change of 100–110 cm, females must mature at a length smaller than ~100 cm and males at a length greater than 100 cm. Thus, female maturity probably occurs somewhere in the length range 75–100 cm TL and age range of ~12–20 years. Males are presumably mature and reproductively competent soon after they make the transition from females, at ~25 years. However,

we caution that our estimates of age at maturity and age at sex change are based on poor data and that these parameters may vary regionally. Furthermore, in the non-breeding season, the ovaries of female serranids regress and their maturity status can be difficult to assess even when using histological methods.

Fecundity and reproductive rate are not known in *E. daemeli*. They have been anecdotally reported to form spawning aggregations (of fewer than 100 fish) in Australia (Harasti and Malcolm 2013), but this observation dates to when they were much more abundant. For example, ~50 individuals were observed gathering near North Solitary Island in NSW by a spearfisher in the 1960s (second-hand historic verbal record via a NSW Fisheries Officer) and 60 *E. daemeli* were caught in one day by a commercial fisher, also in the 1960s, at a nearby site (oral history record, Bob Howard, New South Wales Department of Primary Industries, unpubl. data). During underwater timed-swim surveys in NSW over the past 6 years, the most *E. daemeli* observed during a single count was 18 individuals in autumn (May), with eight fish seen aggregating and interacting. Two pairs of individuals, with one in each pair over 100 cm TL, had light colouration and were rubbing alongside one another while tilting on their sides. Large, mature *E. daemeli* are common at the Kermadec Islands and although individuals have been seen interacting, possibly during courtship, no spawning aggregations have been reported. Non-spawning aggregations also occur: a group of 19 *E. daemeli* seen at the Kermadec Islands in 2004 appeared to be attracted by an unseen prey organism cornered under a boulder (C. Duffy, pers. comm.).

Epinephelus species produce pelagic eggs in several spawning bouts (Coleman *et al.* 1999) and their pelagic larval stage lasts up to 60 days (Heemstra and Randall 1993; Richardson and Gold 1997), during which time larvae may drift long distances in ocean currents. An Argo global drifter (<http://www.argo.net/>, accessed 11 July 2015) deployed at North Solitary Island in 2013 reached the vicinity of LHI, 550 km away, in less than 60 days (Lumpkin and Pazos 2007), and fish larvae probably recruit to north-eastern New Zealand from Norfolk Island, a distance of ~800 km (Francis and Evans 1993; Francis *et al.* 1999). Nevertheless, larval dispersal to Norfolk Island, and presumably also the Kermadec Islands, from the west may be limited owing to the large distances separating these island groups (van der Meer *et al.* 2013). Despite being 'downstream' of all other populations, the remote Kermadec Islands population may be sustained mainly by self-recruitment. The Kermadecs population must be considered a sink and is unlikely to contribute to the rebuilding of western populations.

Ontogenetic movement patterns

In eastern Australia, several fish species recruit to shallow, inshore nursery and juvenile habitats and then move offshore as they mature and grow (Gillanders 1997; Gillanders *et al.* 2003; Poulos *et al.* 2013). Based on spatial variation in size composition, this ontogenetic shift also appears to occur in *E. daemeli*, at least off mainland Australia. Evidence for movement from inshore habitats to offshore reefs comes from the differences in habitat usage between juveniles and adults described above. Juveniles up to ~30 cm TL mainly inhabit shallow coastal water (~0–5 m) and then progressively move into deeper water

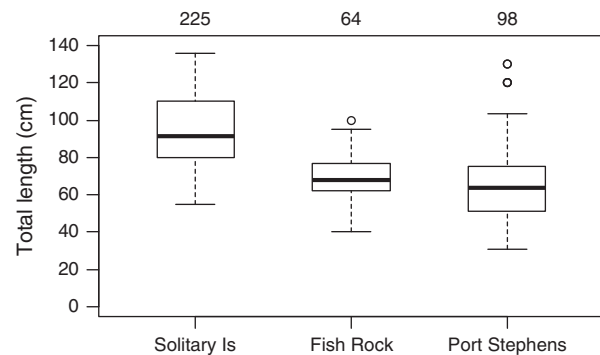


Fig. 6. Variation in length of *Epinephelus daemeli* at three mainland New South Wales (NSW) regions between 2009 and 2014. Regions are listed from north to south, with Solitary Islands being in northern NSW, Port Stephens in central NSW and Fish Rock in between. The thick black lines show median values, the boxes show the interquartile range, the whiskers are $\pm 1.5 \times$ the interquartile range and the circles are outliers. Sample sizes are given at the top of the graph. Data for 2009–12 came from Harasti and Malcolm (2013), whereas unpublished data from the NSW Department of Primary Industries were used for 2013–14.

(~5–25 m) as they grow. There is also evidence of a northward movement along the eastern Australian coastline: *E. daemeli* are generally larger in northern NSW (Solitary Islands) than in two regions in central NSW (Fish Rock and Port Stephens; Fig. 6; Harasti and Malcolm 2013; Harasti *et al.* 2014). Many of the fish from the Solitary Islands would have been mature adults based on their lengths (median length 92 cm, third quartile 110 cm), whereas few individuals longer than 100 cm were recorded south of the Solitary Islands region. Conversely, few fish shorter than 80 cm occurred at the Solitary Islands. One hypothesis to explain these observations is that maturing fish tend to move northwards for reproduction as they grow. A corollary of this hypothesis is that reproduction is largely if not wholly constrained to northern NSW because of a dearth of males (i.e. larger fish) further south. Alternatively, the latitudinal variation in size composition may reflect current or historical higher fishing pressure in the south, resulting in the removal of large old fish from that region.

Diet

Little information is available on the diet of *E. daemeli*. However, it is considered to be an opportunistic carnivore (Leadbitter 1992). Juveniles probably feed on crabs and small fish (Doak 1972; Heemstra and Randall 1993), whereas adults are probably primarily piscivorous, having been caught using live baits such as small scombrids and carangids, as well as artificial lures.

Fisheries bycatch

The New South Wales Department of Primary Industries Recovery Plan for *E. daemeli* identified the NSW ocean trap and line fishery as being a moderate to high risk to this species. Although commercial fishers are not able to retain *E. daemeli* in NSW or Australian Commonwealth waters, bycatch does occur and fish that are released may not survive. Incidental bycatch also likely occurs at Elizabeth Reef (Middleton Reef is a marine sanctuary), LHI, Norfolk Island and northern New Zealand. *Epinephelus daemeli* may suffer mortality from injuries

associated with hooking, handling and attack by sharks. Fish caught from depths greater than ~30 m also suffer barotrauma, and ultimately mortality, even if they are released immediately. This may occur even shallower, because an individual caught by handline in 15 m at the Kermadec Islands was observed to suffer barotrauma (C. Duffy, pers. comm.). Hypodermic puncture of the swim bladder in fish suffering barotrauma may help reduce the mortality of deep-water-caught fish.

Epinephelus daemeli is not protected in Queensland state waters (from the coast to a distance of 3 nautical miles, ~5.6 km, offshore), although it is protected in Commonwealth waters beyond 3 nautical miles. There is some target spearfishing and incidental lining bycatch (both recreational and commercial) in southern Queensland state waters (J. Johnson, pers. comm.).

In New Zealand, few captures of *E. daemeli* are reported by commercial fishers. Francis and Lyon (2012) found only six records of the species in the MPI catch-effort database up to September 2011, but that undoubtedly underestimates the real scale of incidental bycatch. Fish of all sizes are potentially vulnerable to line and set net fisheries operating in rocky reef habitats along the north-east coast of North Island and at the Three Kings Islands. Few fish larger than 100 cm are seen in mainland New Zealand waters (except at the Three Kings Islands), so the vulnerable population components there are mainly juveniles and females.

The Kermadec Islands population of *E. daemeli* is protected within the 12 nautical mile marine reserve ‘bubbles’ that surround the four island groups and encompass all their shallow rocky reef habitat. Thus, this population is not considered to be vulnerable to fishing, other than to any illegal fishing that may occur within the reserve.

Taking *E. daemeli* has been illegal at LHI since 1983, around Elizabeth and Middleton reefs since 1987 and at Norfolk Island since 2012. Middleton Reef has also been a ‘no fishing’ zone since 1987 under the Lord Howe Commonwealth Marine Reserve. There are also ‘no-take’ sanctuaries in the (NSW) LHI Marine Park (since 1999), which provide some additional spatial protection around LHI. The extent of illegal take in these areas is unknown.

Trends in population abundance

Monitoring population sizes of *E. daemeli* is difficult and has only recently been attempted by divers swimming transects across reef habitat and recording fish densities. In NSW, annual surveys of the species commenced in 2009 at several monitoring sites using 45-min timed counts as an index of relative abundance (Fig. 7; Harasti and Malcolm 2013). There was no significant interaction between region and year (generalised linear model using 2010–14 data, $P > 0.05$). Abundance was significantly higher around the Solitary Islands in northern NSW than at Fish Rock and Port Stephens in central NSW ($P < 0.01$), but there was no significant change in abundance over the period 2010–14 ($P > 0.05$). An apparent, although not significant, decline at Fish Rock between 2010 and 2012 can be attributed to excellent underwater visibility early in the time series and poorer visibility subsequently. The Reef Life Survey program has also undertaken surveys in NSW waters between 2008 and 2013 (Edgar and Stuart-Smith 2014). These two survey series

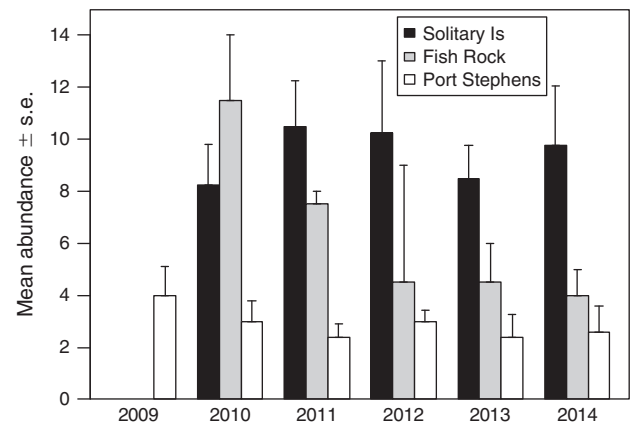


Fig. 7. Mean abundance from 45-min timed underwater counts of *Epinephelus daemeli* at three mainland New South Wales (NSW) regions between 2009 and 2014. Regions are listed from north to south, with Solitary Islands being in northern NSW, Port Stephens in central NSW and Fish Rock in between. Data for 2009–12 came from Harasti and Malcolm (2013), whereas unpublished data from the NSW Department of Primary Industries were used for 2013–14.

will form a strong base for monitoring future changes in abundance in NSW.

At Elizabeth and Middleton reefs, densities of *E. daemeli* declined significantly at four of eight sites surveyed by timed diver swims between 2006 and 2011 (Hobbs *et al.* 2008; Pratchett *et al.* 2011). Other surveys of *E. daemeli* abundance have been performed sporadically. Density estimates have been obtained from surveys at Elizabeth and Middleton reefs in 2003 and 2013 (Oxley *et al.* 2004; Edgar and Stuart-Smith 2014), LHI in 2006 and 2009–12 (Hobbs *et al.* 2009; Edgar *et al.* 2010; Neilson *et al.* 2010; Harasti and Malcolm 2013; Edgar and Stuart-Smith 2014), Norfolk Island in 2009 and 2012 (Edgar and Stuart-Smith 2014; J.-P. Hobbs, Curtin University, pers. comm.) and the Kermadec Islands in 1984, 2008, 2011 and 2012 (Schiel *et al.* 1986; Eddy 2011; Edgar and Stuart-Smith 2014; C. Duffy, unpubl. data). Some of these studies surveyed only a small number of sites and they used a variety of different survey methods, making it difficult to compare abundance estimates over time. Further analysis of these datasets was beyond the scope of the present review but is warranted. Although such surveys are of limited use for monitoring abundance, these abundance estimates may prove useful if they are followed up with further surveys using the same methods in the future. There have been no surveys of *E. daemeli* abundance around mainland New Zealand.

Historical information about *E. daemeli* abundance is typically anecdotal, qualitative or piecemeal, but it may still provide a useful indication of population trends. There is abundant evidence of population decline in the past in NSW as a result of fishing (Pogonoski *et al.* 2002; Marsh 2011; New South Wales Department of Primary Industries 2012). However, it is difficult to gauge whether the population is still declining, stable or recovering because there are no baseline data from before 1983 when the species was protected there. Because the species is slow growing, long lived and matures at a late age, population recovery could take decades. Population declines have also been reported

by local fishers from LHI (Harasti and Malcolm 2013). Adults may have been more common historically, with the low current abundance indicating a lack of recovery following protection.

Conclusions and management implications

The biology, ecology and behaviour of *E. daemeli* make it extraordinarily vulnerable to fishing (Hawkins *et al.* 2000; Dulvy *et al.* 2003; Reynolds *et al.* 2005), along with other large species of *Epinephelus*, such as *E. lanceolatus* and *E. itajara* (Abesamis *et al.* 2014). *Epinephelus daemeli* has an extreme K-selected life history, which minimises its productivity, and habitat and behavioural traits that limit its abundance, even in the absence of fishing. The species is long lived (probably >65 years), late maturing (females mature at ~12–20 years), sex changing (at ~25 years) and it has very specific and limited habitat requirements (rock or coral reef systems with caves and overhangs). Adults, and possibly subadults, may spend their entire lives in the same part of the same reef. Males may defend territories from each other, resulting in a relatively low density. Removal of large, old fish from populations by fishing will skew the sex ratio towards females, potentially compromising reproduction and social hierarchies (Huntsman and Schaaf 1994; Coleman *et al.* 1999; Armsworth 2001). *Epinephelus daemeli* lives in shallow water, usually <50-m depth and often half that. Its restricted geographic range in the south-western Pacific, often around small, steep, isolated islands, and its narrow depth range combine to produce a small total habitat area: it essentially lives in narrow ribbons of reef surrounding the insular parts of its distribution and adjacent to two main coastal regions (NSW and north-eastern New Zealand), both of which currently support only small numbers of fish.

Despite its vulnerability to fishing, management measures implemented by New Zealand and Australia have preserved some *E. daemeli* populations and markedly reduced the effect of fishing on others. Whether depleted populations are recovering remains to be seen and, if they do, recovery may take several decades (Abesamis *et al.* 2014). The Kermadec Islands population appears to be in a near-pristine state, having benefited from the remoteness of the islands, a lack of commercial fishing and the early declaration of a 'no-take' marine reserve (in 1990). The northern New Zealand population is protected by legislation but has never been large; it exists near the latitudinal limit of the species and may not be self-recruiting, relying instead on larval influx from upstream sources such as Norfolk Island and LHI (Francis 1993; Francis and Evans 1993). Populations at LHI, Norfolk Island and Elizabeth and Middleton reefs may have been depleted by early targeted commercial and recreational fishing, followed by incidental recreational catch after the species was protected. The same appears true for the mainland NSW population, which has not shown significant signs of rebuilding in either abundance or size composition since it was protected in 1983, although more frequent anecdotal observations by divers in the Solitary Islands Marine Park are at least positive (H. Malcolm, unpubl. obs.). Targeted and incidental fishing in southern Queensland state waters has undoubtedly reduced the population there to minimal levels, although being at the northern limit of the species' range the population there may never have been large. The key uncertainty now is whether

current fisheries management measures are adequate to prevent further declines in *E. daemeli* abundance and a reduction in reproductive capacity caused by a loss of large males. Legislative protection of the species throughout most of its range has not prevented incidental fishing mortality. Ongoing monitoring is required to determine whether population declines have been arrested and reversed, or whether further protection, for example new or larger 'no take' MPAs and protection in Queensland waters, is required to allow recovery.

Depleted populations of large groupers elsewhere in the world have shown mixed responses to management measures. The endangered *E. striatus* continues to decline in the tropical western Atlantic, despite many measures, including minimum size limits, protection of spawning aggregations and MPAs, being implemented to reduce fishing mortality in parts of its range. However, in some parts of the Caribbean, rigorous protection measures during the spawning season have halted the decline (Whaylen *et al.* 2007; Sadovy de Mitcheson *et al.* 2013). *Epinephelus itajara* has recovered in Florida following a moratorium on its capture in the US since 1990, but recovery has not occurred elsewhere (Sadovy de Mitcheson *et al.* 2013). Groupers are sensitive to even low levels of fishing mortality and recovery of populations, even within 'no-take' MPAs, can take a decade or longer; short bursts of fishing in MPAs can set back their recovery substantially (Abesamis *et al.* 2014). For MPAs to be effective in assisting the recovery of long-lived grouper populations, they must severely reduce or halt fishing mortality for decades and encompass substantial parts of both the juvenile and adult habitat, as well as the migratory corridors and spawning locations for species that aggregate to spawn (Sadovy de Mitcheson *et al.* 2013; Abesamis *et al.* 2014). Other important factors that affect population recovery rates include the size of remnant populations, fishing intensity outside MPAs and recruitment dynamics, including spatial and temporal variability of recruitment and the relationship between larval source and sink populations (Crowder *et al.* 2000; Russ and Alcala 2003; Jones *et al.* 2009; Wen *et al.* 2013).

The NSW recovery plan for *E. daemeli* (New South Wales Department of Primary Industries 2012) details many actions that need to be implemented to ensure the long-term conservation of the species in NSW waters. Specifically, Objectives 1 and 2 of the 'Research & Investigation Activities' focus on collecting data to determine the current and future distribution and abundance of *E. daemeli* in NSW waters in order to inform on population status and assist in determining the effectiveness of recovery actions. Long-term monitoring sites for *E. daemeli* have been established (Harasti and Malcolm 2013) and are being surveyed with a standardised, timed, underwater census method. This should eventually help to determine whether *E. daemeli* is recovering under current management measures.

MPAs along the NSW coast may be important in helping *E. daemeli* populations to recover. Other serranid groupers have benefited from MPAs implemented to curtail fishing (Sedberry *et al.* 1999; Claudet *et al.* 2006; Hackradt *et al.* 2014; Seytre and Francour 2014). In NSW, several key *E. daemeli* locations are partly within MPA 'no-take' sanctuary zones, which help protect their reef habitats and reduce the potential for incidental capture by fishers (Harasti and Malcolm 2013). This includes both North West Rock, which is surrounded by a narrow 100 m

sanctuary, and part of North Solitary Island, where the greatest abundance and largest individuals of *E. daemeli* occur in mainland NSW. However, these small 'no-take' zones do not provide spatial protection for all individuals in these key locations and they take no account of potential migration of fish beyond the MPA boundaries. The production of guidelines for the safe release of captured fish (e.g. best handling practice, barotrauma relief) may also reduce incidental fishing mortality.

Population recovery will probably be influenced by patterns of connectivity among populations. Dispersal of larvae from protected, upstream populations to regions where the populations have not yet recovered is particularly important. Further genetic studies that build on the initial work of van Herwerden *et al.* (2009) will help improve our understanding of the sources of *E. daemeli* larvae and how they recruit to populations elsewhere.

Throughout its range, information on current catch levels of *E. daemeli*, both incidental and illegal, is poor. This results from several factors, including disregard for or ignorance of the protected status of the species, lack of suitable data collection schemes for bycatch and recreational fisheries and the inability of some fishers to identify the species. We have a poor knowledge of the basic biology, ecology and behaviour of *E. daemeli*, and there has been limited monitoring of population sizes. Mortality rates of caught and released fish are unknown, but may be high. In combination, these information shortcomings severely compromise our ability to estimate the current status of *E. daemeli* populations and to forecast expected future trends.

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