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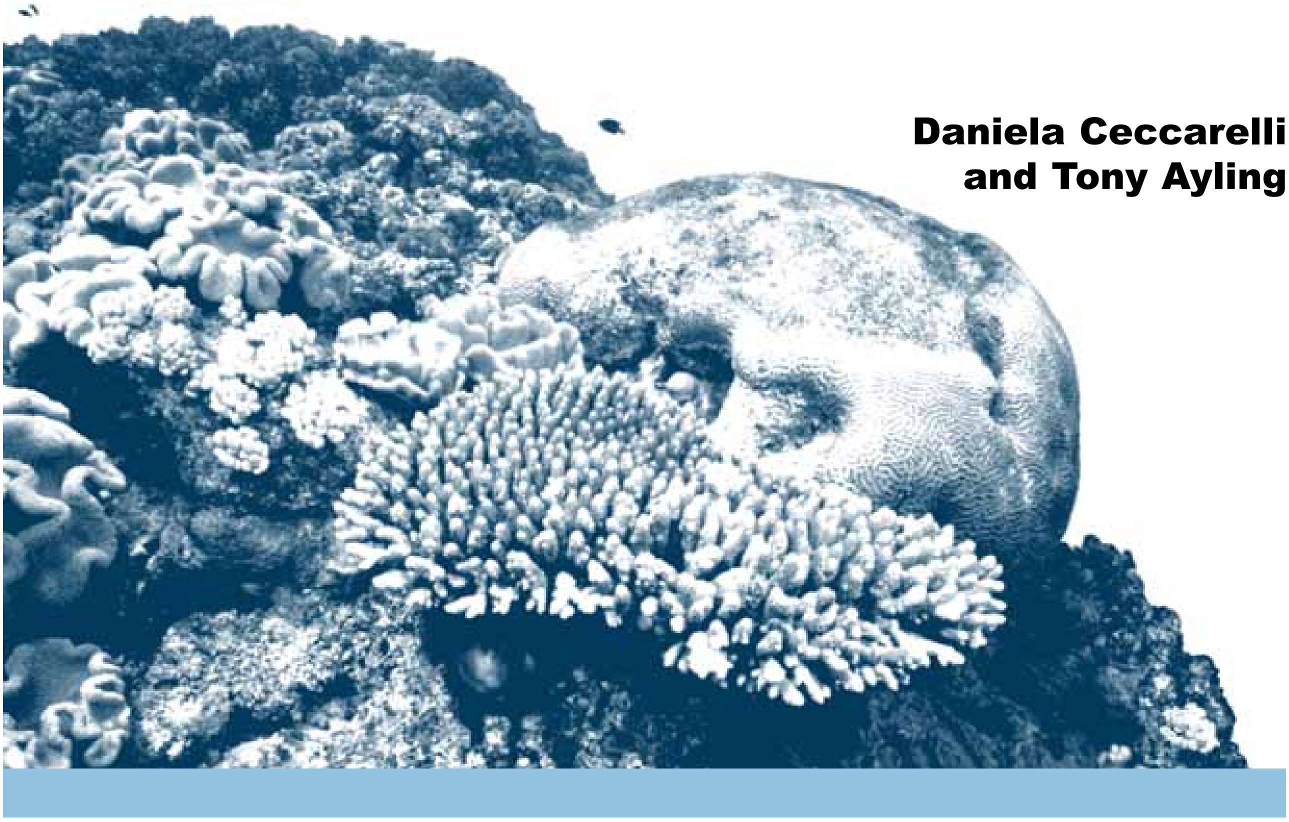

**Daniela Ceccarelli
and Tony Ayling**

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Role, importance and vulnerability of top predators on the Great Barrier Reef – A review

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RESPONSE TO THE REPORT

This report contributes to our knowledge and understanding of the role and importance of apex predators within the Great Barrier Reef Ecosystem. It reinforces that the role of predation in tropical marine ecosystems is complex and spread across a range of species and habitats that are connected in ways that are not well understood. It reinforces the need to verify the status of shark and other important predator populations within the Great Barrier Reef ecosystem.

The Great Barrier Reef Marine Park Authority (GBRMPA) has carefully considered the Report's recommendations and will factor them, as appropriate, into its strategic planning and the ongoing development of research and management priorities in the light of the direction provided by the Outlook Report.

Recommendation GBRMPA	Comment
Improved integration is required between fisheries and ecosystem management and better application of ecosystem-based fisheries management (Pikitch et al. 2004). For instance, a panel charged with reviewing the proposed new management arrangements for the ECIFF [East Coast Inshore Finfish Fishery] considered that this fishery is operating within a MPA [marine protected area] in a World Heritage Area, and the arrangements to protect the sustainability of sharks were not sufficient. However, the new management arrangements included scope for a shark TAC [total allowable catch] of 600t, and for interactions with protected species (Gunn et al. 2008).	When deciding on whether to approve the Wildlife Trade Operation (WTO) for the ECIFF, the Minister set a number of conditions that were aimed at improving the ecosystem-based fisheries management of the ECIFF. Many of these conditions relate to improved protection for high level predators, including sharks.
It is recommended that the GBRMPA assess the viability of establishing a greater number and area of Pink (no-go) Zones on the GBR; recent work on a number of generalist top predators suggests a much better level of compliance in Pink Zones than Green (no-take) Zones. It is recommended that the GBRMPA investigate the viability, cost and logistics of enabling further legislative protection of predators, prioritising species for consideration according to this review's risk assessment.	Other more extensive research has identified that regional variation in the apparent effectiveness of Marine Protected Areas is likely to reflect long-standing regional variations in the amount of fishing and its impacts outside closed areas, rather than wholesale subversion of zoning strategies by high levels of poaching (see quote from Mapstone et al., below). Given this, the GBRMPA considers that focussed education and compliance programs, combined with advances in surveillance technology, will provide a more cost-effective and appropriate solution than increasing the area of Pink (no-access) Zones.
Improved education is required on the importance of green zone compliance. Better enforcement and stricter penalties for infringing on green zones; current levels are not adequately deterring non-	The *GBRMP Act (1975)* has been recently reviewed and a number of amendments were made to increase penalties and strengthen the basis for enforcement. Research and monitoring, including counts

compliant fishers (Ayling & Choat 2008).	of sharks and reef fishes, provides valuable intelligence of hot-spots of non-compliance. This information is being used to target surveillance and education efforts. The GBRMPA is also developing a communication strategy to better promote the overall effectiveness of marine park zoning; not just focussing on no-take zones.

"Surveys of areas that had been open and closed to fishing for over a decade showed that the two main target species of the RLF, the common coral trout and the red throat emperor, were significantly more abundant, larger and older in areas zoned Marine National Park 'B' (and so closed to fishing) than in adjacent General Use areas that have always been open to fishing. The magnitude of these differences varied regionally, from near-zero around Lizard Island to several-fold for some population characteristics in the southern regions of the GBR. The pattern in apparent 'effectiveness' of past closures matched closely patterns in the amount of fishing effort and catch and underlying patterns in the abundances of several harvest and non-harvest species. We present circumstantial arguments that this regional variation in the apparent 'effectiveness' of Marine Protected Areas is likely to reflect long-standing regional variations in the amounts of fishing and its impacts outside closed areas, rather than wholesale subversion of zoning strategies by high levels of poaching. That is, the lack of contrast between open and closed areas in the Lizard Region probably arises because the open areas are lightly fished, whereas the strong contrasts in the other regions arises because of relatively heavy fishing in the open areas in those regions."

Quote from Mapstone et al. (2004) *The effects of line fishing on the Great Barrier Reef and evaluations of alternative potential management strategies*. Technical Report No. 52, CRC Reef research Centre, Townsville.

Research recommendation (quoted verbatim)	**Proposed response**
Effective censuses of the status and catch of those species prioritised through the risk assessment (especially those falling into the 'extreme' and 'very high' risk categories are an essential first step towards understanding the current status of the most important predators on the GBR. This would help to determine which species are undergoing the greatest decline, and assist in further prioritising limited resources for more detailed biological and ecological studies.	The recommended research would potentially advance the knowledge base pertaining to the conservation status of apex predators in the Marine Park. However, the need for the research must be considered in the context of existing research priorities, which are outlined in the document titled "Scientific information needs for the management of the Great Barrier Reef Marine Park 2009 – 2014".
Distribution, abundance and life-history data is required for many of the predator species. Some of this research is underway for some species, but it needs to be completed for all exploited GBR sharks as a priority. It is suggested that research on individual species be prioritised according to this review's importance index and / or risk	The recommended research would potentially advance the knowledge base pertaining to the threats and risks to apex predators in the Marine Park. However, the need for the research must be considered in the context of existing research

assessment. Research on individual species, particularly sharks, should include: - *Life history and habitat use information for all species, especially those caught by fisheries and prioritising the most 'at risk';* - *Logbooks and observer programs that distinguish between species as much as possible. Better effort and catch data for all species across all fisheries, with better and more regular reporting mechanisms;* - *Records of how many sharks a year are taken as by-catch;* - *Determine overall GBR exploitation rates of 'at risk' species including all fisheries and sectors, and deaths from other factors;* - *Better understanding of post-release survival rates from all sectors, including charter;* - *Develop a list of potential no-take species based on the least productive sharks caught by all fisheries. This will help identify where there is not enough knowledge to make a species 'no-take' and direct research on particular species.* -	priorities, which are outlined in the document titled "Scientific information needs for the management of the Great Barrier Reef Marine Park 2009 – 2014".
It is recommended that a targeted research program be developed to specifically undertake ecosystem-level comparisons between different zones, including reef and non-reef habitats. Factors to consider for such a research program include: - *Making use of large-scale latitudinal gradients and cross-shelf gradients in anthropogenic pressure;* - *Incorporating gradients in fishing pressure within areas open to fishing;* - *Incorporating zoning-related gradients in fishing pressure (long-term monitoring of no-go Pink Zones embedded within large no-take Green Zones may provide the best tool for understanding ecosystems where predator densities are most likely to be at 'natural' levels);* - *Considering all the GBR's major habitat types: coral reefs, inshore and inter-reef areas, pelagic and deep-water environments. Research has begun to target non-coral reef areas and a future program on the role of predators on the GBR will benefit from incorporating the*	The recommended research would potentially advance the knowledge base pertaining to the functional role of apex predators in an ecosystem setting, and the ecological consequences of over-exploiting apex predators in the Marine Park. However, the need for the research must be considered in the context of existing research priorities.

expertise of researchers that are already examining these systems; - *Using current accepted sampling designs that allow sufficient replication at all levels, and that take into account sampling techniques relevant to the species and to the habitat (e.g. visual surveys are useful in clear water, while tagging studies and catch data may be more efficient in inshore turbid waters and remote techniques are suitable for deep water);* - *Selecting a wide range of ecosystem response variables, including potential prey species, competitors, key functional groups such as herbivores, invertebrate feeders and macro-invertebrates, habitat structure and complexity, and the community composition of benthic organisms.*	

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Executive Summary

The purpose of this review is to evaluate the ecological role of predators on the Great Barrier Reef (GBR), their vulnerability to human activities and their contribution to ecosystem and economic values. Marine systems around the world are under increasing pressure, from the localised anthropogenic impacts of fishing and terrestrial run-off to the global pressures of climate change. There is concern over exploitation and declining numbers and biomass of large marine predators, worldwide and on the GBR. Understanding the role of predation and the consequences of predator loss is a priority for managers. To better understand the link between the protection of exploited fish stocks, the enhancement of the GBR's overall resilience and the maintenance of ecosystem structure and function, this review seeks to answer the following questions:

1. What is the role and importance of apex predators on the GBR and other tropical marine ecosystems?
2. What is the status and vulnerability of apex predators on the GBR?
3. What is the contribution of apex predators to the GBR's ecosystems and anthropogenic values?
4. How is the role of apex predators expected to change under predicted climate change?

For the purposes of this review, 115 species of top-level predators are recognised within the GBR. They are separated into three categories:

- Apex predators (22 species) are large (250cm or greater maximum total length), and feed almost exclusively on other large marine animals (cetaceans, seabirds, turtles and other predators). They have extensive ranges and move freely between habitats.
- Generalist top predators (67 species) are smaller (50-250cm maximum total length), but still have a proportion of other piscivores in their diet (at least 30%). They range from species that move freely between habitats – albeit not as extensively as apex predators – to species that undertake habitat shifts during their life cycle (ontogenetically), to those that are relatively sedentary.
- High-level mesopredators (26 species) include species of varying sizes that are of high trophic level (Trophic Index ~4) and are important predators in their respective ecosystems. The diets of these species include a high proportion (at least 50%) of squid or fish, but not necessarily other piscivores.

An extensive literature and data review was carried out to evaluate the current knowledge of the role of predators in tropical marine ecosystems, and in the GBR in particular. The species within each category were assessed and ranked in order of relative importance and vulnerability. A risk assessment was then carried out to assist in the prioritisation of species or groups of species for research, management and conservation measures. The risk assessment, combining importance and vulnerability rankings for each species, resulted in the following five species ranking highest in each category:

- Apex predators: tiger shark *Galeocerdo cuvier*, bull shark *Carcharhinus leucas*, scalloped hammerhead *Sphyrna lewini,* swordfish *Xiphias gladius*, and great hammerhead *S. mokarran*.
- Generalist top predators: whitetip reef shark *Triaenodon obesus*, black shark *Daliatis licha,* Taiwan gulper shark *Centrophorus niaukang*, common blacktip shark *Carcharhinus limbatus* and albacore *Thunnus alalunga.*

- High-level mesopredators: giant moray *Gymnothorax javanicus*, giant trevally *Caranx ignobilis,* escolar *Lepidocybium flavobrunneum*, humphead Maori wrasse *Cheilinus undulatus* and mahi mahi *Coryphaena hippurus*.

Generalist top predators and high-level mesopredators are often of greater local importance than apex predators. Site-attached sharks, such as the three species of reef sharks (grey reef shark *Carcharhinus amblyrhynchos*, blacktip reef shark *C. melanopterus* and whitetip reef shark *Triaenodon obesus*), and large cods and groupers are some of the most important generalist top predators on coral reefs, while tunas and billfish perform an important role in the pelagic system, and sharks specialised to utilise inshore habitats are likely to affect coastal and inter-reef areas to a greater degree.

Predation is one of the key biological forces structuring abundance, recruitment, species composition, diversity and behaviour of prey. Direct effects of predators on prey often have indirect consequences for species and communities of lower trophic levels. However, there is very little empirical evidence about the role and importance of apex predators. The role of predation in structuring ecosystems is generally derived from studies on species from the more site-attached generalist top predator and high-level mesopredator groups. The role of predators is clearer in simpler ecosystems, where empirical evidence and theoretical models show that the removal of top consumers is likely to result in large-scale ecosystem changes. On the GBR, the only direct evidence of this is the reduction of corallivorous starfish in Green Zones, where predators are protected.

The GBR's predators are of high value to the Great Barrier Reef Marine Park (GBRMP)'s tourism and fishing industries, and are valued socially and culturally for their iconic status and their position in the social and spiritual systems of the indigenous groups inhabiting the GBR coast. Diving tourism on the GBR relies heavily on the presence of large predators, especially sharks, and it is argued that the value of large predators to tourism is much greater than their fisheries value. Fisheries operating within the GBRMP target a high proportion of predators, and evidence of the sustainability of capturing predators at current exploitation levels is equivocal.

Concern over the depletion of top predators around the world is exacerbated by the scant knowledge and lack of consensus about the effects of their disappearance on ecosystems. There is little or no information on the overall ecosystem difference between areas with and without 'healthy' populations of predators on the GBR. Furthermore, the success of Pink (no entry) Zones in protecting shark populations is hampered by their rarity; they make up only 1% of the area of the GBRMP. Further research is required to verify the status of shark populations on the GBR and to assess what level of harvest, if any, can be sustained without endangering those populations.

There is a great deal of uncertainty about the combined effects of future environmental conditions predicted under climate change and the depletion of large predators. For the GBR's ecosystems to recover from disturbances caused by predicted conditions of higher temperatures, lower pH and greater variability in storm frequency and intensity, salinity and current systems, they require a certain level of resilience, or the capacity to return to their previous state. Recent research has shown that areas protected from fishing, either by remoteness or legislation, host greater numbers of large predators than fished areas. A number of studies have shown a link between higher predator densities and greater complexity, higher coral cover and lower pest and disease susceptibility. Therefore, preliminary evidence suggests that top predators play an important role in maintaining resilience. It is recommended that management and conservation measures be strengthened, especially for sharks. Furthermore, a research program is suggested to answer the question: what happens to GBR ecosystems when predators are removed?

INTRODUCTION

Predation is one of the key biological forces shaping ecological communities (Almany et al. 2007). 'Apex' or 'top' predators are those animals at the top of a food chain that have little or no likelihood of being eaten themselves. These predators are usually larger in size and fewer in number than their prey (Jennings et al. 2001; Otto et al. 2007) and are situated at the tip or 'apex' of a pyramid-shaped representation of relative abundance in food webs (Figure 1). Apex predators are said to control ecosystems 'from the top down' by regulating prey populations and by indirectly affecting trophic levels further down the food web (Baum & Worm 2009). Removing top predators is said to have 'cascading' effects on all the components of a food web or chain (Heithaus 2001a; Baum & Worm 2009; Ings et al. 2009). Large-bodied apex predators therefore can have far-reaching direct and indirect effects on ecological communities disproportionate to their abundance (Stevens et al. 2000).

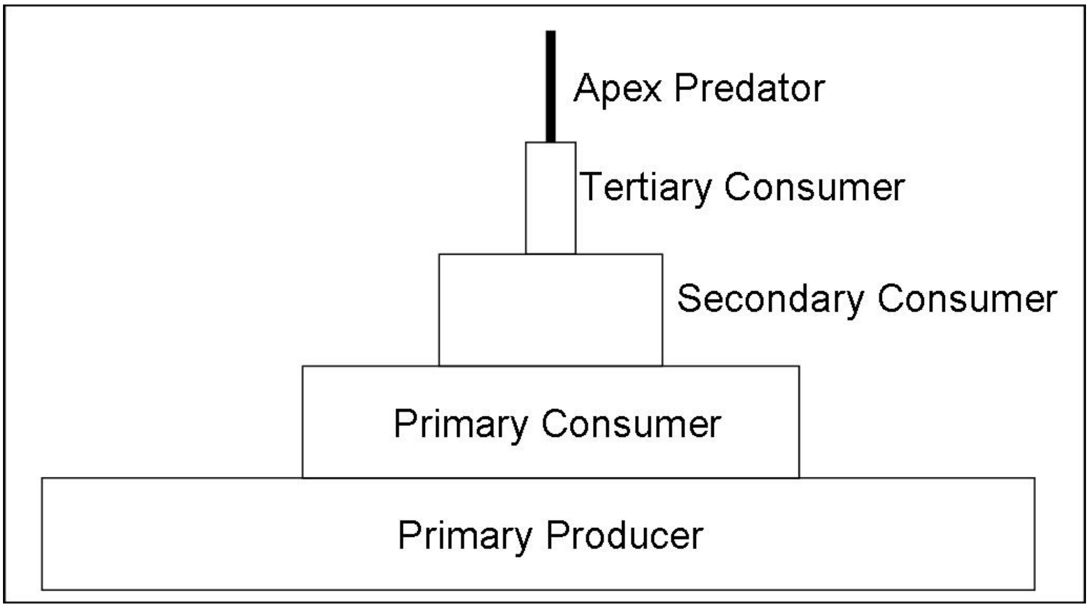

Figure 1. Schematic diagram of trophic pyramid, representing decrease in abundance and stored energy from lower to higher trophic levels.

The role and importance of apex predators has been studied in terrestrial (e.g. Terborgh et al. 2001), freshwater (e.g. Woodward & Hildrew 2001) and marine systems (Almany et al. 2007). Most studies and reviews have found that marine food webs are complex and often further affected by the physical and structural nature of the ecosystem. This is especially true of the tropics, where the complex nature of marine ecosystems presents numerous confounding factors to studies attempting to determine the effects of predation. A review of experimental work shows that top-down control of coral reef communities by predation, for instance, interacts closely with bottom-up effects of resource and refuge availability (Heck & Valentine 2007). Furthermore, the understanding of the ecosystem-level effects of predation is in its infancy, as most studies have been conducted experimentally at small spatial scales. However, there is general agreement that healthy ecosystems should sustain a full complement of functional groups, including top predators, and that the integrity of these functional groups is a central component of ecosystem resilience (Bellwood et al. 2004).

Marine systems around the world are under increasing pressure from localised anthropogenic impacts of fishing and terrestrial run-off and the global pressures of climate change and pollution (Gardner et al. 2003; Hoegh-Guldberg et al. 2007; De'ath et al. 2009). Extending along Australia's most populated coastline, the Great Barrier Reef (GBR) is no exception. Recent analyses of the GBR's vulnerability to climate change found that the combined effects of a number of pressures will require active management strategies to increase the GBR's resilience (Johnson & Marshall 2007). While climate change predictions are subject to uncertainty, the expected conditions affecting marine ecosystems are expected to be largely detrimental.

The GBR's key functional groups, loosely defined as a collection of species that perform similar ecological roles irrespective of their taxonomic relationship, include habitat-forming corals, seagrasses and other benthic organisms, mobile macroinvertebrates, grazing fish and large-bodied predators (Bellwood et al. 2004). Recent research has shown the importance of protecting coral reef grazers due to their role in removing macroalgal biomass and therefore mediating coral dominance on the GBR (Hughes et al. 2003). However, while in developing countries there is a real concern over the loss of herbivorous fishes, on the GBR it is primarily large-bodied predators that are targeted by both commercial and recreational fisheries. Apex predators are regarded by some as crucial or 'keystone' components of ecosystems, and current knowledge suggests that they contribute substantially to trophodynamics[1] (ICES 2006). However, compared to the role of herbivores on coral reefs, the importance of apex predators in tropical marine ecosystems is not well understood (Dulvy et al. 2004a).

There is concern over a reported decline of over 90% of marine predators worldwide (Jackson et al. 2001; Myers & Worm 2003). Despite the lack of consensus about the role of apex predators, the loss of any functional group from shallow marine ecosystems is expected to reduce the resilience of that ecosystem to large-scale impacts (Hughes et al. 2002; Dulvy et al. 2004a). Given the long-term and intense exploitation of predators on the GBR and in other marine systems (Pauly et al. 1998a; Myers & Worm 2003; McCann 2007; Coll et al. 2008), understanding the role of predation, and therefore the consequences of losses in predator populations, is a priority for managers (Almany et al. 2007).

Fishing on the GBR is regulated by Queensland State fisheries regulations and through a Marine Park zoning system designed for multiple use and ultimately aiming to protect biodiversity. Just over 30% of the Great Barrier Reef Marine Park (GBRMP) is currently protected in no-take zones, spanning a range of reef and non-reef ecosystems. This globally accepted management strategy has been proven numerous times to successfully protect exploited species. More recently, effective protection is expected to support the natural resilience of coral reefs to exploitation and disturbance (Diaz-Pulido et al. 2009). However, the role of no-take zones in protecting large-bodied apex predators is poorly understood. Furthermore, understanding the effectiveness of this type of protection for enhancing the overall resilience of the GBR to climate change is still in its infancy. To better understand the link between the protection of exploited predators, the enhancement of the GBR's overall resilience and the maintenance of ecosystem structure and function, it is important to ask the following questions:

1. What is the role and importance of apex predators on the GBR and other tropical marine ecosystems?

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[1] Trophodynamics relates to the patterns of energy transfer between levels of a food chain or web, also called trophic levels.

2. What is the status and vulnerability of apex predators on the GBR?
3. What is the contribution of apex predators to the GBR's ecosystems and anthropogenic values?
4. How is the role of apex predators expected to change under predicted climate change?

OBJECTIVES AND SCOPE

In recognition of the GBR's vulnerability to climate change, the Australian Government through the Great Barrier Reef Marine Park Authority (GBRMPA) is implementing the Great Barrier Reef Climate Change Action Plan 2007-2012 (Action Plan). This Action Plan outlines a coordinated response to the threat of climate change for the GBR, whereby enhancing the resilience of the GBR ecosystem is an integral component of the Action Plan. Understanding the influence of predators on the structure and dynamics of healthy marine ecosystems will assist the development of effective management strategies for this functional group.

The primary objective of this study is to prepare an independent report about the importance of predators in the GBR ecosystem, and evaluate their vulnerability to current and future pressures. The scope of the project is a desktop review including a synthesis of available information, an evaluation of threats and risks affecting predator populations on the GBR, and recommendations about the conservation and management of predators. The specific objectives of this project are to:

- assess the role and importance of predators in the GBR ecosystem,
- evaluate the threats and risks to predators in the GBR ecosystem, including
  - the impacts on predator populations themselves, and
  - the impacts of predator depletion on ecosystem functioning, trophodynamics and resilience to climate change, and
- provide recommendations regarding the conservation and sustainable use of predators in the GBR ecosystem.

This information will help determine the priority needs for management of predators, and help ensure long-term ecosystem resilience of the GBR in the face of current and future human impacts and climate change.

Methods

This study consisted of a review of available literature and data, and a risk assessment designed to prioritise top predator species in most need of future research or conservation.

Literature and Data Search

This project involved an intensive search for relevant information on the effects of predators on tropical marine ecosystems in general and on the GBR in particular. Estimates of 'natural' predator population sizes and distributions were sought, as well as threats and human impacts on predators and the flow-on effects on ecosystems. Emphasis was placed on information specific to the GBR, for both reef and non-reef habitats. This literature search contributed to both the general discussions on the importance of predators and to the compilation of species-specific information used in the calculation of importance and vulnerability indices (see pages 15-17). Data on predator species distribution and abundance and on fisheries catch rates were requested from relevant agencies. Material that was considered for this study included:

1. Pertinent published and unpublished reports;
2. Peer-reviewed literature;
3. Media releases and newspaper articles;
4. Web-based material and databases (e.g. FishBase);
5. Data from Queensland's Shark Control Program;
6. Species-specific fisheries catch data and maps;
7. Information used to compile the 2007 Climate Change Vulnerability Assessment of the Great Barrier Reef (Chin & Kyne 2007);
8. Australian Intitute of Marine Science (AIMS) Long Term Monitoring Program data;
9. Annual Status Reports of Great Barrier Reef fisheries; and
10. Spatial habitat data for the Great Barrier Reef.

Interviews and Expert Advice

Relevant experts and government agencies were approached for data, published and unpublished reports, leads to further material, and (where no actual data were available) anecdotal evidence. Agencies and persons approached included:

1. GBRMPA (data and reports only);
2. Fisheries Queensland (formerly DPI&F) (data and reports only);
3. The Australian Fisheries Management Authority (AFMA; data and reports only);
4. Fishing & Fisheries Research Centre, JCU;
5. CSIRO; and
6. Experts on fisheries biology, coral reef ecology, the GBR and other relevant fields.

Species List and Individual Species Profiles

The suite of predators considered here is based on species that are known to occur in the GBR Region, and that are considered to have a minimal likelihood of serving as prey as adults. Limiting the definition to adults circumvents the problem of ontogenetic[2] shifts in the predator-prey role, where large individuals of a smaller, non-apex species

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[2] Relating to the different stages of an organism's life history

can feed on small – usually juvenile – individuals of larger species (Woodward & Hildrew 2002b). It is recognised that most marine species grown indeterminately (ie. there is no maximum size), and that their trophic level increases with size (Text Box 1).

Text Box 1. Size, abundance and the trophic pyramid.

In marine communities, size determines both abundance and trophic level. The relationship between abundance and mass is generally to the power of -3/4 (within a trophic level) and is steeper in multitrophic communities due to predation, as follows:

$$A = M^{-0.75} * M^{TE/PPMR}$$

where TE is transfer efficiency (~10%) and PPMR is predator prey mass ratio (typically 300-1000:1)

Additionally, biomass scales as:

$$B \sim M^{0.25} * M^{TE/PPMR}$$

An interpretation of these relationships is that there are fewer large-bodied individuals at higher trophic levels, but at the same time standing biomass is greater in these largest size classes. The classic trophic pyramid is therefore correct if it represents a time-averaged community, but if a time-slice were taken, the result would be an inverted biomass pyramid.

An important question to consider then becomes whether the time slice or the time averaged ecosystem is more representative of the overall ecosystem dynamics. Recent theory suggests it is more important to have the largest size classes represented, irrespective of the identity of the species in these large size classes (Jennings & Mackinson 2003; Dulvy et al. 2004b).

Species considered apex or top predators in recent studies on marine trophodynamics were considered (e.g. Friedlander & DeMartini 2002), including most sharks, large carangids (trevally), groupers, barracuda, snappers, emperors, tunas and billfish. Sharks are widely considered to be apex predators, except for smaller species and those that feed on benthic invertebrates (Stevens et al. 2000). Additionally, we used the Marine Trophic Index (MTI) as a guideline for including or excluding species (Pauly & Watson 2005). This Index was originally devised to provide a guideline for assessing the trophic level of fishes, primarily as a fisheries tool, and is recorded in the FishBase database (www.fishbase.org) for thousands of species. The MTI ranges in value from 1 to 5, with larger numbers denoting higher trophic levels (Bhathal & Pauly 2008). For the purposes of this review, the cut-off point for top-level predators was set at 4; species ranking below this value were excluded unless otherwise explained. Size also played a part in identifying top-level predators, although it is not often a good indicator of trophic level (Jennings et al. 2001). Generally, species were not included if their adult total length was below 50cm. The list considered here includes species conforming to at least two of the following three criteria:

1. Species with a Trophic Level, as defined by the MTI, of 4 or above; and / or
2. Species commonly considered top-level or apex predators in the peer-reviewed literature, including through the results of stable isotope analysis (e.g. Revill et al. 2009); and / or
3. Species recorded as having piscivores in their diet.

Recent research by the CSIRO on oceanic predators established four broad trophic groupings: higher predators, generalist top predators (sharks, tuna and billfish), mid-level predators (e.g. albacore, dolphin fish) and mid-level prey (e.g. myctophids, small scombrids). The higher, or apex, predators were identified as large, mobile sharks (e.g. mako sharks) (Revill et al. 2009). These groupings were applied to the selected list of

GBR predators for this review. The three predator groupings are therefore defined as follows:

- **Apex predators** are large (250cm or greater maximum total length), and feed almost exclusively on other large marine animals (cetaceans, seabirds, turtles and other predators). They have extensive ranges and move freely between habitats.
- **Generalist top predators** are smaller (~50-250cm maximum total length), but still have a proportion of other piscivores in their diet (at least 30%). They range from species that move freely between habitats – albeit not as extensively as apex predators – to species that undertake ontogenetic habitat shifts, to those that are relatively sedentary.
- **High-level mesopredators** include species of varying sizes that have high trophic levels (~4) and are known to play important predatory roles in their respective ecosystems. The diets of these species include a high proportion (at least 50%) of squid or fish, but not necessarily other piscivores.

Common names of predators considered in this report are those suggested in the CSIRO list of standard common names for Australian fish species (see http://www.cmar.csiro.au/caab/).

To evaluate the areas over which the different predator species might influence GBR ecosystems, previously established bioregions of the GBR were used to identify broad habitat categories. Fisheries catch data, documented distributions, knowledge of preferred habitats and the author's (Dr Tony Ayling) own experience were used in combination to define the spatial extent of probable occurrence for each species or species group. Species distributions were mapped according to bioregions of the GBR, supplied by GBRMPA. Distributions of many predators are poorly known; but where available they were taken from the AIMS Long Term Monitoring Program data, Last and Stevens (2009), shark control and fisheries catch data and individual studies. Overlays were created with the fisheries catch data, obtained directly from QPIF and indirectly through the web-based search tool Coastal Habitat Resources Information System (http://chrisweb.dpi.qld.gov.au/chris/). Numbers of sharks of each species caught between 1996 and 2006 by the Queensland Shark Control Program were also mapped. In order to define and justify the final list of apex predators and a selected group of generalist top predators chosen for this study, each species was profiled with known information about their biology, life history, ecology, distribution and abundance.

Data Management

The primary dataset compiled for this study included (where available) relative abundance, distribution, life history parameters, diet, trophic level, fisheries catch information and qualitative and semi-quantitative assessments of importance and vulnerability for each species. Additionally, a map of the GBR's bioregions was manipulated to depict likely distribution patterns. Where primary or published sources were not available, information was obtained from FishBase (www.fishbase.org).

Data from the AIMS Long Term Monitoring Program and from studies on individual species were requested from relevant agencies and scientists (e.g. Fishing & Fisheries Research Centre, JCU). The Long Term Monitoring Program data were primarily used to identify distribution and abundance patterns for relevant species. Additionally, species lists and vulnerability indices were provided by the authors of the Chonrichthyan chapter of the Great Barrier Reef Vulnerability Assessment (Chin & Kyne 2007). The existing Vulnerability Assessment indices were further developed to include the non-chondrichthyan predators assessed in this study (see below).

Fisheries catch data were obtained from the Queensland Department of Primary Industries and Fisheries (QPIF), both directly (catch data 2005-2008), through the online Coastal Habitat Resources Information System search and mapping tools (catch data up to 2005) and from the publically available Annual Status Reports. Where possible, data were summarised for each of the identified species of apex predators, generalist top predators, and high-level mesopredators by year and by location (according to the grid system used by QPIF). Resulting maps were overlayed onto maps of known distribution of species on the GBR to provide a spatial overview of potential exploitation hotspots for individual species.

Data on numbers of sharks caught by the Queensland Shark Control Program were obtained online (QPIF 2008) and directly from relevant QPIF personnel. Only data from locations within the GBRMP area were considered.

Importance Index

Three factors were combined for each species to produce an ‘importance index’ with which to rank the species within each of the three groups, with rank increasing with higher abundance. The following criteria contributed to the index:

- Abundance or density – it is expected that species occurring in higher abundance on the GBR will contribute more to overall ecosystem function than rare species (Brewer et al. 1995; Gaston & Fuller 2008)(see also ‘size’). Abundance was represented as a relative rank, based on comparison of species abundances in individual studies, fisheries catch data, and Queensland shark control data. For reef dwelling species abundance data from the AIMS Long Term Monitoring Program and the Effects of Line Fishing (ELF) Experiment visual count program was combined with other available abundance data to derive an overall mean adundance per 100 hectares (ha). Adundance data from north, central and southern GBR regions, where available, was averaged to get a GBR-wide average abundance. For inshore species catch data from the shark control program was combined with catches from the East Coast Inshore Finfish Fishery (ECIFF) to get an average relative ranking for each species that was converted to an estimated density using available quantitative data for other species. Pelagic species were ranked using data from the Eastern Tuna and Billfish Fishery (ETBF) from areas just outside the GBRMP. Once again relative rankings were converted to an abundance ranking by reference to known quantitative data.
    - Abundance ranking for reef dwelling species was relatively accurate, as a considerable amount of density data was available for many species (see list of data sources). Reef frequenting pelagic species abundance was estimated relative to reef dwelling species based on observations at many different reef sites and habitats over a period of many decades.
    - There are some shortcomings with the abundance estimates for inshore and offshore species groups. The catch data used are almost certainly selective both with regard to size and species and probably do not give an accurate estimate of relative ranking, especially for species at the smaller end of the size scale. However, it is generally the larger species that are the most important in the overall ranking, and relative catch rates of these large species probably reflect actual abundance differences.
    - The shark control program catch is probably most biased toward large species / individuals, but even in this fishery about half the catch was sharks less than 2 m in length.

  - Although rankings within the three major habitat types are relatively robust, comparing abundance estimates across all habitats probably leads to some inconsistencies. However, as long as some consideration is given to the overall importance of predators within each habitat then the limitations of the data are not insurmountable. It is also important to base estimates of abundance on actual data where possible, in spite of the limitations and preliminary nature of that which is available.
  - Due to the large difference between the least and most abundant species of generalist top predators and high-level mesopredators (three orders of magnitude), abundance estimates were log10-transformed before ranking, and then ranked from one to 12. Apex predators were ranked separately in recognition of their higher trophic role, and the data range was not of a magnitude that required transformation.
- Size – a size factor was used in conjunction with the abundance ranking to determine importance, as it is expected that larger predators will have greater effects than smaller species. Larger species and individuals tend to be correlated with a higher proportion of fish in their diet (Kulbicki et al. 2005), and trophic level is positively correlated with size (Jennings & Mackinson 2003), and therefore larger species and individuals are likely to have greater impacts on lower trophic levels. Size estimates were obtained from FishBase and sources listed in Table 2. Size was then ranked from 1 to 12.
- The MTI was used as an initial guideline for including or excluding species, and then species-specific diet and trophic information were used to further refine the list and to rank the species within each list. If further information about a species was found that contradicted the position as top-level predator (as indicated by the MTI) the species was excluded even if its MTI was four or above. Once MTIs were assigned to all the chosen species, they were also ranked between one and twelve (by calculating the number from 1 to 12 on a linear scale) to maintain consistency.

In an effort to maintain a simple analysis, the 1-12 rankings for the three criteria above were multiplied to give an importance index for each species.

Vulnerability Index

Each species was also assessed according to its vulnerability to threats from human activities, including direct exploitation through fisheries and anthropogenic impacts to its environment. The vulnerability index was developed in accordance with the method employed by Chin and Kyne (2007), with additional information on life history and exploitation level. Calculating vulnerability therefore consisted of the following components:

- Ranking each attribute of sensitivity and adaptive capacity as low, moderate or high, for each species, as per Chin and Kyne (2007)(see Text Box 2). These rankings were then applied to a fisheries-style risk assessment, which multiplies the individual component rankings to produce a final outcome that describes the vulnerability of that species. The level of sensitivity or inadaptability is rated as 0.33 (low), 0.66 (moderate) or 1.00 (high). When multiplied, these ratings produce a vulnerability ‘index’ ranging from 0.00 to 1.00, where 0.00 to 0.33 equals low vulnerability, 0.34 to 0.66 equates to moderate vulnerability, and 0.67 to 1.00 equates to high vulnerability (Chin & Kyne 2007).

- In addition to the Chin & Kyne (2007) method, measures of 'vulnerability' as calculated by FishBase (see www.fishbase.org for details on equations), that express intrinsic levels of vulnerability to exploitation based on individuals species' life histories, were ranked and used as multipliers (Cheung et al. 2005; Reynolds et al. 2005).

The vulnerability index developed here is therefore designed to combine information on the intrinsic vulnerability of each species (given its life history parameters) with its vulnerability to direct pressure (from fishing) and pressure on its habitat (from climate change).

Text Box 2. Explanation of sensitivity and adaptive capacity used in Chin and Kyne (2007).

Measures of 'sensitivity' and 'adaptive capacity' for this study were largely adopted from Chin and Kyne (2007). A species' sensitivity was defined as its ability to resist or adapt to change. Sensitivity was defined by two attributes:

1. Rarity – rarer species have smaller populations and may have lower genetic variation and a lower net reproductive output, inhibiting their ability to recover from mortality events. Rarer species are therefore more sensitive than abundant ones.
2. Habitat specificity – species restricted to particular habitats may not be able to compete effectively in other habitats. Their lack of flexibility in exploiting different habitats makes them more sensitive to disturbances.

Adaptive capacity is defined as the ability to adapt to disturbance of mortality events without the risk of extinction. To integrate this 'positive' attribute with the other 'negative' characteristics, each component of adaptive capacity is also expressed in negative terms. Adaptive capacity was defined by four attributes:

1. Trophic specificity – species that depend on specific types of prey are less adaptable, and therefore have high inadaptability.
2. Physical or chemical intolerance – species with physiological traits that allow them to tolerate a wide range of physical and chemical conditions such as salinity or temperature have low inadaptability.
3. Immobility – species incapable of travelling large distances have high inadaptability.
4. Latitudinal range (proxy for temperature intolerance) – species that can be found across a large latitudinal range are probably tolerant of a range of temperatures, and therefore have low inadaptability.

The sensitivity and inadaptability of each species were ranked as low, moderate or high.

Risk Assessment

The importance and vulnerability indices were combined to provide a semi-quantitative risk index to assist in prioritising species for management and conservation (Table 1). The importance index contains information of the relative abundance, size and trophic level of each species. The vulnerability index combines relative rankings of each species' sensitivity, inadaptability and intrinsic vulnerability based on life history characteristics. Multiplying the two indices for each species produced a risk level; all risk levels were then ranked as Extreme (>100), Very high (75-100), High (50-74), Moderate (25-49), Low (1-24) or Negligible (<1).

Table 1. Risk assessment table using importance and vulnerability to evaluate levels of risk for each species.

Species	Importance Index			x	Vulnerability Index			=	Risk
(eg.)	Abundance rank	Size rank	Trophic rank		Sensitivity	Inadaptability	Vulnerability (intrinsic)		
Tiger shark (*Galeocerdo cuvier*)									
Common coral trout (*Plectropomus leopardus*)									

Impacts of Climate Change

Attempting to predict the impacts of climate change on apex predators of the GBR and the consequences of apex predator exploitation under a range of climate change effects, requires an understanding of the potential responses of apex predators to the key environmental characteristics that are predicted to change. To this end, current knowledge of the vulnerability of apex predators to changes in water temperature, ocean acidity, salinity, storm frequency and ocean circulation were briefly summarised.

The potential scenario used for this report was taken from widely accepted, peer-reviewed predictions already available in the scientific literature (Hoegh-Guldberg et al. 2007). The potential responses of GBR predators to this scenario were determined by assessing their vulnerability (through the Vulnerability Index) under current exploitation levels against the prospect of widespread habitat changes.

Limitations and Assumptions

- Sizes of predators were obtained from Last and Stevens (2009) for elasmobranchs, Corkeron (1994) for cetaceans, and FishBase (Froese & Pauly 2009) for teleosts.

- Distribution and abundance data was very limited for most species. Abundance estimates are therefore presented as relative abundance ranks, based on individual studies, data and observations of Dr. Tony Ayling, AIMS Long Term Monitoring Program data, and catch data from fisheries operating inside or just outside the GBRMP boundaries (e.g. the Eastern Tuna and Billfish Fishery, ETBF) and from the Queensland Shark Control Program. Distribution data are also derived from a combination of these sources.
- The available fisheries catch data generally had poor species resolution and all catch data is likely to be affected by the selectivity of the gear.
- Despite the establishment of a set of clear guidelines for the separation of species into the three predator categories, the decision about inclusion or exclusion of species will always have a subjective and arbitrary element.
- The indices used here to calculate relative importance and vulnerability are simple; more complex models may produce different results. However, all quantitative evaluations, be they simple index calculations or complex ecological models, are only as accurate as the data used. Therefore, to refine the rankings and assessments, a priority must be targeted data collection. The risk assessment is designed to help prioritise species for which such data collection may be most urgent.
- There is limited empirical evidence of the role of predators on the GBR, so much of the information was inferred from elsewhere.
- Many of the studies on reef fish dynamics in general, and on the effects of predation in particular, have been undertaken experimentally at small spatial scales (usually 10s to 100s of meters). The effects documented by these studies may not accurately reflect the effects of predators at ecosystem-level scales (kilometres to 1000s of kilometres). In order to define some of the potential effects of predators, results of small-scale studies have been extrapolated where necessary. Small-scale experiments are cited here in the absence of larger-scale studies, in the recognition that future work is needed at appropriate scales.

The Role of Apex Predators in Tropical Marine Ecosystems

While it is generally agreed that predation is a major structuring force in marine communities, there is little empirical evidence about the role of predation in complex tropical marine ecosystems. The best evidence for top-down predator control of aquatic systems comes from lakes; marine communities appear too complex and diverse for the detection of clear interactions (Stevens et al. 2000). In the tropics, apex predators often exist within species-rich ecosystems such as mangroves, seagrass beds, soft-bottom benthic communities and coral reefs. Small-scale experiments using constructed patch reefs have shown predation to be one of the key mechanisms structuring the abundance, behaviour and community composition of coral reef fishes, but the ecosystem-level effects of predators remain largely untested. The role of predation has been at the centre of the question of density-dependence in reef fish communities (Carr et al. 2002). It is thought that predation exerts direct top-down control both through density-dependent and behaviour-mediated interactions (Bascompte et al. 2005; Preisser et al. 2005; Papastamatiou et al. 2009). On coral reefs, predation and competition often need to be considered synergistically, and the combined effects of these two processes are said to contribute significantly to the maintenance of the relative abundance of prey, biodiversity and community stability at small spatial scales (Carr et al. 2002).

The general responses to predation include reductions in abundance of preferred prey at large scales (DeMartini et al. 2008), while at smaller spatial scales predators cause higher survival rates of unpreferred prey (Almany et al. 2007), changes in overall size composition (Connell 1998), reductions in size at sexual maturity or sex change (DeMartini et al. 2008), changes in sheltering behaviour (Stallings 2008), feeding behaviour (Heithaus & Dill 2006), social structure (Heithaus 2001a) and changed interactions among prey species (Almany 2004). Empirical evidence of the role and importance of apex predators in the tropics relates primarily to coral reefs, with less information available for soft-bottom communities, inshore areas and the offshore pelagic environment. Because of the difficulties in studying relatively rare, large-bodied and wide-ranging animals (Wirsing et al. 2007b), most existing information focuses on the more site-attached species at small spatial scales. Predator-prey interactions are clearest near the top of the food chain, introducing further difficulty in assessing the effects of predation on lower trophic levels (Stevens et al. 2000).

In some ecosystems, predators perform ‘keystone’ roles, maintaining overall biodiversity by selectively targeting superior competitors; but empirical evidence of this comes from relatively simple ecological settings (Stevens et al. 2000; Brose et al. 2005). These settings have provided for both theoretical and empirical evidence that the depletion of top predators frees intermediate consumers from population control, and the effects of these changes are propagated down the food web and throughout the community (Stevens et al. 2000; Okey et al. 2004; Shepherd & Myers 2005; Ward & Myers 2005; Frid et al. 2008). Large sharks are most often identified as keystone species in tropical and subtropical marine systems (Libralato et al. 2006). For example, the overfishing of large sharks off North Carolina that led to a dramatic increase in prey (primarily mesopredatory elasmobranchs such as rays) which then decimated bivalve stocks and brought about the collapse of the scallop fishery (Myers et al. 2007). Little empirical evidence exists from complex systems where the relationship between apex predators and their environment is still poorly quantified and understood (Wirsing et al. 2007b). However, recently reviewed evidence suggests that top predators can exert strong control on ecosystem in both simple and complex systems (Heithaus et al. 2008a). Because apex predators are often large, mobile species that can connect communities, food webs and habitats that are otherwise spatially segregated (Woodward & Hildrew 2002a) they may create linkages that contribute to ecosystem stability (Rooney et al. 2006).

Given the predominance of apex predators targeted by fisheries, opportunities for directly measuring predation effects are diminishing as fish communities in their natural state become increasingly rare (DeMartini et al. 2008). Indeed, much of our knowledge about the importance of apex predators in ecosystems comes from studying the consequences of apex predator removal (Myers et al. 2007). The ecosystem effects of overfishing apex predators can be far-reaching, but have only recently become part of modelling studies and fisheries research (Myers & Worm 2003). Furthermore, knowledge about the importance of predation in structuring tropical communities comes from observations of site-specific phenomena (Heithaus et al. 2007a), small-scale experiments on coral reefs, and more recently from larger-scale empirical observations in the Pacific (Dulvy et al. 2002; DeMartini et al. 2008). Even in complex systems, however, it is highly likely that the loss of an entire functional group will bring about ecosystem change (Stevens et al. 2000; Myers et al. 2007).

Issues of Scale

The ecosystem role of predators is difficult to evaluate because the effects of predation are not usually measured at the appropriate scale. The results of small-scale experiments that have informed much of the knowledge of the effects of predation on corals reefs may not be applicable at a larger scale. At least one study has found that spatial scale influences whether benthic community structure is primarily driven by bottom-up (turf density) or top-down (predation) factors (Dulvy et al. 2002). Typically, large-scale studies tend to define patterns and relationships between predator and prey communities (e.g. Friedlander & DeMartini 2002; DeMartini et al. 2008), while the mechanisms by which predation affects reef communities have only been tested at small scales (e.g. Carr et al. 2002; Almany et al. 2007; Stallings 2008). The issue of scale pertains both to primary literature and to reviews. Many literature reviews themselves contain a large number of small-scale studies (e.g. Heck & Valentine 2007), on which broader inferences are based. It is recognised that while predation or predation risk may change the abundance, distribution, feeding behaviour or recruit survival of prey over small scales and short timeframes, this may not be equally important at population or community scales.

Direct Effects

The direct effects of apex predators include the influence on prey survivorship, abundance, distribution, behaviour and population dynamics (Graham et al. 2003; DeMartini et al. 2008; Heithaus et al. 2008b). Localised predator-mediated reduction in prey abundance has been shown to be especially common during settlement of recruiting fish (Almany & Webster 2006; Stallings 2008). Predation can also affect species diversity (Almany et al. 2007) and behaviour (Heithaus & Dill 2006). Increasing predation has been found to lead to three potential patterns of species diversity: 1) no change, 2) monotonic decrease, or 3) highest diversity at intermediate levels of predation intensity (Hixon 1991). In the third possibility, predation pressure emulates the frequency and intensity of disturbance in the intermediate disturbance hypothesis, in that species diversity is highest under intermediate predation pressure (Connell 1978). No change or a monotonic decrease in prey diversity may be present in high-diversity systems, such as coral reefs, where smaller or unidentifiable prey differences could lead to lower selectivity in predators (Almany et al. 2007).

Changes in behaviour of prey in direct response to predation include increased sheltering behaviour, changes in social structure, changes in foraging or feeding behaviour (Heithaus et al. 2007a; Wirsing et al. 2007a; Stallings 2008) and in some cases, costly defensive strategies (Preisser et al. 2005). Changes in behaviour relative to the risk of predation may be greatest in large-bodied and long-lived prey, such as sea turtles, where the consequences of a premature death to an individual's fitness may be particularly detrimental (Heithaus et al. 2008b). For instance, research in Western Australia has shown that adult sea turtles may avoid areas favourable for feeding to avoid the risk of predation by large tiger sharks (Heithaus et al. 2008b).

The cost of modified behaviour to prey species can include reduced energetic investment in reproduction, lower reproductive success, decreased energy intake and increased vulnerability to other predators. A recent review by Preisser et al. (2005) suggests that the impact of predation on prey densities through intimidation is as great, if not greater, than that of direct consumption. They suggest that trophic interactions between predators and prey, and the flow-on effects on the surrounding ecosystem, may in fact be the dominant facet of trophodynamics.

Indirect Effects

Indirect effects of predators can be as strong, and more far-reaching in terms of the magnitude of the affected species, as their direct reduction in prey abundance through consumption (Heithaus et al. 2008a). However, they can be more difficult to define and quantify, especially in complex ecosystems (Heck & Valentine 2007). Indirect interactions,mostly defined for small spatial scales, can include predator-mediated changes in abundance or behaviour of species lower in the food web, termed 'density-mediated' and 'trait-mediated', respectively (Stallings 2008). The importance of density-mediated indirect effects of predators are often highlighted when fisheries selectively remove predators or competitors in a way that leads to species replacement, and local enhancement of food supply through discards (Stevens et al. 2000). The most commonly known indirect consequence of a change in predation pressure is the 'trophic cascade', where dramatic alterations in species composition or abundance 'cascade' through the ecosystem into lower trophic levels (Pinnegar et al. 2000).

Trophic Cascades

While many indirect interactions exist between predators and lower trophic levels (Stevens et al. 2000), trophic cascades are perhaps the most dramatic. This occurs when the effect of removing predators from the top of a food web has repercussions throughout the whole ecosystem and is most easily demonstrated in systems with three trophic levels (Pinnegar et al. 2000). Generally, when apex predators are removed, their direct prey increases, which in turn depletes resources further down the food web (Pinnegar et al. 2000; Dulvy et al. 2004a). The loss of apex predators has been linked to the degradation of whole ecosystems (Bascompte et al. 2005; Ferretti et al. 2008). Marine evidence for trophic cascades exists for kelp forests (e.g. Carter et al. 2007), rocky intertidal systems (e.g. Menge 2000), oceanic environments (e.g. Baum & Worm 2009), rocky reefs (e.g. Shears & Babcock 2002; Clemente et al. 2007; Sonnenholzner et al. 2009) and coral reefs (e.g. Pinnegar et al. 2000; Dulvy et al. 2004a; Mumby et al. 2006; McClanahan et al. 2007; Mumby et al. 2007; Sweatman 2008).

The removal of apex predators such as sharks has resulted in the collapse of at least one invertebrate fishery (Myers et al. 2007). There is some uncertainty about whether a higher degree of functional redundancy exists in more complex and diverse systems, providing a buffer against trophic cascades (Myers et al. 2007). For instance, on coral reefs the evidence of trophic cascades exists from relatively low-diversity systems such as Caribbean and Kenyan reefs (Jennings & Kaiser 1998; McClanahan et al. 2007). Some researchers argue that trophic cascades are equally possible in low and high diversity systems, but the greater functional redundancy inherent in high-diversity systems means that the loss of individual predator species may have lower repercussions than in low-diversity systems (Heithaus et al. 2008a). It has also been shown that protection from fishing can reverse the ecosystem-wide effects of trophic cascades (Shears & Babcock 2002).

Perhaps the best-documented trophic cascade in the tropics has been the overgrowth of coral reefs by fleshy macroalgae as a result of herbivore removal (Pinnegar et al. 2000), and more recently the cascading effects of predator protection in reducing the impacts of corallivorous starfish (Sweatman 2008). It is unclear what the role of apex predators is in this regard. Intuitively, it is expected that the removal of apex predators would lead to the increased density of herbivores; however, recent evidence suggests that marine protected areas designed to protect predators also lead to increased populations of large herbivores (Dulvy et al. 2002; Friedlander & DeMartini 2002; Nardi et al. 2004). The occurrence of trophic cascades in soft-bottom communities has received less attention, and while it has been found that predators decrease the density and diversity of benthic assemblages, a history of trawling activities in many areas is likely to confound the role of predation (Pinnegar et al. 2000).

‘Natural’ Densities of Apex Predators

The difficulty in identifying the role and importance of marine predators is compounded by the lack of ecosystems where predator populations can be considered intact (Myers & Worm 2003; Paddack et al. 2009). There is widespread consensus that based on historical data and accounts, large predators were present in much greater densities (by some accounts, 10-20 times greater) than they are today (MacIntyre et al. 1995; Pauly 1995; Sandin et al. 2008). Some researchers maintain that the depletion of large predators was already taking place before the onset of record-keeping and research (Jackson et al. 2001). Steele and Schumacher (2000) ask the question: what were marine ecosystems like before intensive fishing?

The concepts of ‘fishing down marine food webs’ (Pauly et al. 1998a) and the ‘shifting baseline’ (Pauly 1995; Dayton 1998) are frequently cited as major impediments to evaluating ‘natural’ fish densities (Myers & Worm 2003). As the population of the largest species are depleted, fisheries tend to focus on progressively smaller species (Christensen & Pauly 1998). It is not possible to ascertain the potential carrying capacity of ecosystems once major functional groups have been virtually removed, but modelling suggests that current ecosystems are degraded, not carrying their full capacity and therefore not producing optimal catch rates for fisheries (Christensen & Pauly 1998; Jackson et al. 2001). Additionally, severely depleted functional groups cannot perform their ecological role, leading to an ecosystem that functions differently (Myers et al. 1997; Jackson et al. 2001). Even measurements of ecosystem recovery after long-term protection cannot determine with any certainty whether a protected system is eventually able to re-attain its natural state (McClanahan et al. 2007).

A theoretical basis for predicting the baseline densities of predators has been developed by Jennings et al. (2008), including the estimation of global teleost and elasmobranch biomass. However, even they admit that the main limitation of their analysis “… was the absence of an approach for rigorously predicting the relative contributions of teleost or elasmobranch biomass to total biomass when data were sparse and fishing has modified contemporary food webs.” In a more empirical approach, comparisons between fished, no-take and no-go zones on the GBR carried out by Robbins et al. (2006) give an indication of potential baseline densities of reef sharks between 80 and 97% higher than presently occurring on fished reefs.

A number of recent studies have identified areas of very low historic fishing pressure, where fish communities could be considered ‘natural’. Surprising patterns have emerged from the trophic structure of reef fish on ‘pristine’ coral reefs. On unfished coral reefs of Hawaii and the Line Islands, Friedlander and DeMartini (2002) and DeMartini et al (2008) reported ‘inverted’ trophic pyramids where reef fish biomass was dominated by predators such as sharks, large trevallies and snappers. The abundance and size of large predators in Hawaii was much greater on unfished than on fished islands – predators made up 54% of the fish biomass on unfished reefs and only 3% on fished reefs (Friedlander & DeMartini 2002; Stevenson et al. 2007). Whether these patterns are applicable to other tropical marine systems is yet to be determined.

APEX PREDATOR SPECIES OF THE GBR

GBR Apex Predator Species List

Our assessment of GBR predators included 115 species of predators, including 22 apex predators, 67 generalist top predators and 26 high-level mesopredators (Table 2). This distinction allows for the inclusion of all major predators of other piscivores, but acknowledges the difference between the very large (~250 cm and above) predators of cetaceans and sharks, smaller species (~50-250cm) that nevertheless play a major predatory role at a more localised scale and include a large proportion (30% and above) of other piscivores in their diet, and species of a high trophic level that occupy important predatory roles within specific habitats. While the trophic level, as determined by the MTI, is given for each species, additional dietary information and general considerations about trophic roles found in the literature are supplied, together with the relevant information sources. This additional dietary information was cross-referenced against the trophic level of each species to provide the justification for its inclusion.

To evaluate the areas over which the different predator species might influence GBR ecosystems, broad habitat categories were identified for each species. Most apex predators range across a variety of habitats, but on the GBR all predators can be roughly divided into coral reef, inshore and inter-reef, pelagic and deep-water predators (Table 2). The apex predators are often habitat generalists, ranging across GBR habitats with only limited preferences for particular areas.

Generalist top predators are much more likely to be site-attached within individual habitats than the wider-ranging apex predators. In this category, very few species' occurrences span the continental shelf and the latitudinal extent of the GBR. However, there are also very few habitat specialists, with many species occurring in both reef and inter-reef habitats. Species are more likely to be segregated across the shelf (ie. inshore, mid shelf or outer shelf / offshore) than along latitudinal gradients (ie. occurring primarily north or south of a given point). Many of the species in the high-level mesopredator category are coral reef specialists.

Table 2. Species assessed in this review, including the functional groups (FG) apex predators (A), generalist top predators (G) and high-level mesopredators (M) including their trophic level (TL and associated standard error or S.E.), maximum published total length in cm, justification for inclusion and relevant sources of information. General habitat preferences are also given. Phylogenetic groups (PG) include: Elasmobranchs (E), teleosts (T), reptiles (R) and cetaceans (C). Note: the bronze whaler shark, *Carcharhinus brachyurus*, is sometimes considered as occurring in the GBR Region, but the latest distribution information from Last and Stevens (2009) suggests otherwise. SIA: Stable Isotope Analysis; SI N: Stable Isotope Nitrogen.

FG	PG	Family	Species	Common Name	TL (SE)	Max L (cm)	Justification	References	Habitat
A	E	Carcharhinidae	*Carcharhinus albimarginatus*	Silvertip shark	4.48 (0.77)	280	Piscivores and elasmobranchs in diet	FishBase	Pelagic, coral reef
	E	Carcharhinidae	*Carcharhinus altimus*	Bignose shark	4.5 (0.75)	300	Feeds on other piscivores, incl. elasmobranchs	(Stevens & McLoughlin 1991)	Deep water
	E	Carcharhinidae	*Carcharhinus amboinensis*	Pigeye shark	4.29 (0.65)	280	Top predators, prey on cetaceans	(Heithaus 2001a)	Inshore, coral reef
	E	Carcharhinidae	*Carcharhinus falciformis*	Silky shark	4.5 (0.65)	300	Piscivores in diet	FishBase	Oceanic
	E	Carcharhinidae	*Carcharhinus leucas*	Bull shark	4.34 (0.84)	300	Top predators, prey on cetaceans and other elasmobranchs	(Heithaus 2001a; Myers et al. 2007)	Inshore, coral reef
	E	Carcharhinidae	*Carcharhinus longimanus*	Oceanic whitetip shark	4.39 (0.74)	400	Top predators, prey on cetaceans	(Heithaus 2001a)	Oceanic
	E	Carcharhinidae	*Carcharhinus obscurus*	Dusky shark	4.61 (0.82)	365	Top predators, prey on cetaceans and other elasmobranchs	(Heithaus 2001a; Myers et al. 2007)	Pelagic, inshore, coral reef
	E	Carcharhinidae	*Carcharias taurus*	Greynurse shark	4.44 (0.82)	320	Feeds on other piscivores, inc elasmobranchs	(Lucifora et al. 2009b)	Inshore
	E	Lamnidae	*Carcharodon carcharias*	White shark	4.53 (0.65)	600	Top predators, prey on cetaceans and other elasmobranchs	(Heithaus 2001a; Myers et al. 2007)	Pelagic, nearshore pelagic, coral reef
	R	Crocodylidae	*Crocodylus porosus*	Estuarine crocodile	~5	600	Commonly known as marine/estuarine apex predator	(QPWS 2007)	Inshore, coral reef
	E	Carcharhinidae	*Galeocerdo cuvier*	Tiger shark	4.42 (0.91)	600	Top predators, prey on cetaceans and other elasmobranchs	(Heithaus 2001a; Myers et al. 2007)	Inshore, pelagic, coral reef, deep water
	E	Lamnidae	*Isurus oxyrhinchus*	Shortfin mako	4.32 (0.78)	400	Top predators, prey on cetaceans and other elasmobranchs	(Heithaus 2001a; Myers et al. 2007; Revill et al. 2009)	Pelagic, nearshore pelagic
	E	Lamnidae	*Isurus paucus*	Longfin mako	4.5 (0.8)	430	Top predator by SIA	(Revill et al. 2009)	Pelagic, nearshore pelagic

FG	PG	Family	Species	Common Name	TL (SE)	Max L (cm)	Justification	References	Habitat
	T	Istiophoridae	*Makaira indica*	Black marlin	4.47 (0.79)	465	Billfish as top predators, piscivores in diet	(Christensen & Pauly 1998; Myers & Worm 2003; Bachok et al. 2004)	Pelagic, nearshore pelagic
	T	Istiophoridae	*Makaira mazara*	Indo-Pacific blue marlin	4.46 (0.89)	500	Billfish as top predators	(Christensen & Pauly 1998; Myers & Worm 2003)	Pelagic, nearshore pelagic
	E	Carcharhinidae	*Negaprion acutidens*	Lemon shark	4.13 (0.67)	310	Piscivores in diet	(White et al. 2004)	Inshore, Coral reef
	C	Delphinidae	*Orcinus orca*	Orca	4.5	800	Commonly known as marine apex predator	(Pauly et al. 1998b)	Pelagic
	C	Delphinidae	*Pseudorca crassidens*	False killer whale	4.5	600	Preys on other cetaceans and large tunas	(Pauly et al. 1998b)	Pelagic
	E	Sphyrnidae	*Sphyrna leweni*	Scalloped hammerhead	4.21 (0.68)	350	Top predators, prey on cetaceans and other elasmobranchs	(Heithaus 2001a; Myers et al. 2007)	Inshore, coral reef, pelagic
	E	Sphyrnidae	*Sphyrna mokarran*	Great hammerhead	4.43 (0.81)	610	Top predators, prey on cetaceans and other elasmobranchs	(Heithaus 2001a; Myers et al. 2007)	Inshore, coral reef, Pelagic
	T	Istiophoridae	*Tetrapturus audax*	Striped marlin	4.50 (0.77)	420	Billfish as top predators	(Christensen & Pauly 1998)	Pelagic, nearshore pelagic
	T	Xiphiidae	*Xiphias gladius*	Swordfish	4.46 (0.64)	455	Top predator by SIA, stomach contents	(Moteki et al. 2001; Revill et al. 2009)	Pelagic, nearshore pelagic, deep water
G	T	Scombridae	*Acanthocybium solandri*	Wahoo	4.42 (0.92)	250	Feeds on other piscivores	FishBase	Pelagic
	E	Alopiidae	*Alopias superciliosus*	Bigeye thresher	4.47 (0.76)	488	Feeds on large pelagic piscivores, inc. billfish	FishBase	Deep water, pelagic
	E	Carcharhinidae	*Carcharhinus amblyrhinchos*	Grey reef shark	4.5 (0.74)	225	Reef sharks listed as tertiary/apex predators	(Friedlander & DeMartini 2002; DeMartini et al. 2008)	Coral reef
	E	Carcharhinidae	*Carcharhinus amblyrhynchoides*	Graceful shark	4.22 (0.69)	160	Piscivores in diet, inc other sharks	(Stevens & McLoughlin 1991; Salini et al. 1994)	Pelagic
	E	Carcharhinidae	*Carcharhinus brevipinna*	Spinner shark	4.5 (0.78)	233	Prey on other sharks	FishBase	Pelagic, inshore
	E	Carcharhinidae	*Carcharhinus cautus*	Nervous shark	4.47 (0.79)	150	Piscivores in diet	(White et al. 2004)	Inshore
	E	Carcharhinidae	*Carcharhinus dussumieri*	Whitecheek shark	3.9 (0.63)	82	Piscivores in diet	(Salini et al. 1994)	Inshore, Deep water

FG	PG	Family	Species	Common Name	TL (SE)	Max L (cm)	Justification	References	Habitat
	E	Carcharhinidae	*Carcharhinus fitzroyensis*	Creek whaler	4.05 (0.65)	135	Piscivores in diet	(Lyle 1987)	Inshore
	E	Carcharhinidae	*Carcharhinus limbatus*	Common blacktip shark	4.24 (0.69)	255	Top predators, prey on cetaceans and other elasmobranchs	(Heithaus 2001a; Myers et al. 2007)	Pelagic, nearshore pelagic
	E	Carcharhinidae	*Carcharhinus macloti*	Hardnose shark	4.18 (0.67)	85	Piscivores in diet	(Stevens & McLoughlin 1991)	Pelagic, inshore
	E	Carcharhinidae	*Carcharhinus melanopterus*	Blacktip reef shark	4.33 (0.67)	200	Reef sharks listed as tertiary/apex predators	(Friedlander & DeMartini 2002; DeMartini et al. 2008)	Coral reef, inshore
	E	Carcharhinidae	*Carcharhinus plumbeus*	Sandbar shark	4.49 (0.79)	250	Top predators, prey on cetaceans and other elasmobranchs	(Heithaus 2001a; Myers et al. 2007)	Pelagic, deep water
	E	Carcharhinidae	*Carcharhinus sorrah*	Spot-tail shark	4.15 (0.64)	160	Piscivores in diet	(Salini et al. 1994)	Inshore, Pelagic
	E	Carcharhinidae	*Carcharhinus tilstoni*	Australian blacktip shark	4.23 (0.68)	200	Piscivores in diet	(Salini et al. 1994)	Inshore, Pelagic
	E	Centrophoridae	*Centrophorus niaukang*	Taiwan gulper shark	4.5 (0.8)	160	Feeds on other piscivores	FishBase	Deep water
	E	Centrophoridae	*Centrophorus moluccensis*	Endeavour dogfish	4.33 (0.7)	100	Feeds on other piscivores, inc elasmobranchs	FishBase	Deep water
	E	Dalatiidae	*Dalatias licha*	Black shark	4.3 (0.82)	182	Feeds on other piscivores, inc elasmobranchs	FishBase	Deep water
	E	Echinorhinidae	*Echinorhinus cookei*	Prickly shark	4.39 (0.76)	400	Feeds on fish, cephalopods, other sharks	FishBase	Deep water
	T	Serranidae	*Epinephelus coioides*	Goldspotted rockcod	3.95 (0.67)	120	Feeds on fish	(Randall 2005)	Coral reef, inshore
	T	Serranidae	*Epinephelus fuscoguttatus*	Flowery rockcod	4.14 (0.72)	120	Identified as a top predator	(Pears et al. 2006)	Coral reef, inshore
	T	Serranidae	*Epinephelus lanceolatus*	Queensland groper	4 (0.6)	270	Recorded as eating elasmobranchs	(Randall 1977)	Coral reef, inshore
	T	Serranidae	*Epinephelus malabaricus*	Blackspotted rockcod	4.16 (0.61)	234	Feeds on some piscivores	FishBase	Coral reef, inshore
	T	Serranidae	*Epinephelus polyphekadion*	Camouflage grouper	4 (0.55)	90	Not much information - seems to feed on small fish and crustaceans	FishBase	Coral reef, inshore
	T	Serranidae	*Epinephelus tukula*	Potato rockcod	4.2 (0.68)	200	Feeds on some piscivores	FishBase	Pelagic, nearshore pelagic
	E	Sphyrnidae	*Eusphyra blochii*	Winghead shark	4.05 (0.61)	186	Feeds on other piscivores, inc elasmobranchs	FishBase	Oceanic

FG	PG	Family	Species	Common Name	TL (SE)	Max L (cm)	Justification	References	Habitat
	T	Scombridae	*Euthynnus affinis*	Mackerel tuna	4.47 (0.8)	100	Piscivores in diet	(Griffiths et al. 2009)	Pelagic, nearshore pelagic
	T	Gempylidae	*Gempylus serpens*	Snake mackerel	4.35 (0.7)	100	Top predator by SIA	(Revill et al. 2009)	Oceanic
	C	Delphinidae	*Globicephala melas*	Long-finned pilot whale	4-5	760	Feeds mainly on squid	DEWHA-SPRAT	Oceanic
	E	Carcharhinidae	*Glyphis glyphis*	Speartooth shark	Not given	175	More information required		Inshore
	T	Scombridae	*Gymnosarda unicolor*	Dogtooth tuna	4.5 (0.75)	248	Feeds primarily on planktivores	FishBase	Coral reef, pelagic
	E	Hemigaleidae	*Hemipristis elongata*	Fossil shark	4.27 (0.59)	230	Piscivores in diet, inc other sharks	FishBase	Deep water
	E	Hexanchidae	*Heptranchias perlo*	Sharpnose sevengill shark	4.27 (0.64)	140	Feeds on other sharks and piscivores	(Braccini et al. 2005)	Deep water
	E	Hexanchidae	*Hexanchus makanurai*	Bigeye sixgill shark	4.42 (0.71)	180	Top predators, prey on cetaceans	(Heithaus 2001a)	Deep water
	E	Triakidae	*Hypogaleus hyugaensis*	Pencil shark	4.24 (0.7)	127	Feeds on piscivores	(Simpfendorfer et al. 2002a)	Deep water
	T	Istiophoridae	*Istiophorus platypterus*	Sailfish	4.5 (0.79)	350	Piscivores in diet	FishBase	Pelagic, nearshore pelagic
	T	Lutjanidae	*Lutjans bohar*	Red bass	4.11 (0.7)	90	Listed as tertiary predator	(DeMartini et al. 2008)	Coral reef
	E	Orectolobidae	*Orectolobus maculatus*	Spotted wobbegong	4.23 (0.64)	170	Feeds on reef fish and octopus	(Last & Stevens 2009)	Coral reef
	T	Serranidae	*Plectropomus areolatus*	Passionfruit coral trout	4.5 (0.8)	75	*Plectropomus* species listed as major predators	(Graham et al. 2007)	Coral reef
	T	Serranidae	*Plectropomus laevis*	Bluespotted coral trout	4.14 (0.57)	125	*Plectropomus* species listed as major predators	(Graham et al. 2007)	Coral reef
	T	Serranidae	*Plectropomus leopardus*	Common coral trout	4.41 (0.96)	120	*Plectropomus* species listed as major predators	(Graham et al. 2007)	Coral reef
	T	Serranidae	*Plectropomus maculatus*	Barcheek coral trout	4.11 (0.7)	75	*Plectropomus* species listed as major predators	(Graham et al. 2007)	Coral reef
	E	Carcharhinidae	*Prionace glauca*	Blue shark	4.37+/-0.83	400	Top predators, prey on cetaceans, SIA	(Heithaus 2001a; Revill et al. 2009)	Pelagic, nearshore pelagic
	E	Carcharhinidae	*Rhizoprionodon acutus*	Milk shark	4.33 (0.76)	110	Piscivores in diet	(Salini et al. 1994; White et al. 2004)	Inter-reef, deep water
	E	Carcharhinidae	*Rhizoprionodon taylori*	Australian sharpnose shark	4.5 (0.8)	70	Feeds on piscivores	(Stevens & McLoughlin 1991)	Inter-reef, deep water
	T	Scombridae	*Scomberomorus commerson*	Spanish mackerel	4.38 (0.74)	240	Piscivores in diet	(Bachok et al. 2004)	Pelagic, nearshore pelagic

FG	PG	Family	Species	Common Name	TL (SE)	Max L (cm)	Justification	References	Habitat
	T	Scombridae	*Scomberomorus semifasciatus*	Grey mackerel	4.5 (0.8)	120	Feeds on piscivores	(Blaber 1986)	Pelagic, nearshore pelagic
	T	Sphyraenidae	*Sphyraena barracuda*	Great barracuda	4.5 (0.8)	220	Estuarine piscivore, SI N Value of 11.7-11.9	(Abrantes & Sheaves 2009)	Coral reef, inshore, pelagic
	T	Sphyraenidae	*Sphyraena jello*	Pickhandle barracuda	4.29 (0.68)	150	Piscivores in diet	(Bachok et al. 2004)	Coral reef, inshore, pelagic
	T	Sphyraenidae	*Sphyraena qenie*	Blackfin barracuda	4.5 (0.8)	140	Not much information, but probably similar to other sphyraenids		Coral reef, pelagic
	E	Squalidae	*Squalus montalbani*	Philippine spurdog	4.35 (0.80)	95	Feeds on other piscivores	FishBase	Deep water
	E	Squalidae	*Squalus megalops*	Piked spurdog	4.24 (0.71)	71	Feeds on fish and other elasmobranchs	(Braccini et al. 2005)	Deep water
	T	Istiophoridae	*Tetrapturus angustirostris*	Shortbill spearfish	4.50 (0.76)	230	Billfish as top predators	(Christensen & Pauly 1998)	Oceanic
	T	Scombridae	*Thunnus alalunga*	Albacore	4.13 (0.74)	140	Tunas as top predators	(Christensen & Pauly 1998; Myers & Worm 2003; Baum & Worm 2009)	Oceanic
	T	Scombridae	*Thunnus albacares*	Yellowfin tuna	4.48 (0.93)	239	Tunas as top predators, SIA, stomach contents	(Christensen & Pauly 1998; Myers & Worm 2003; Baum & Worm 2009)	Oceanic
	T	Scombridae	*Thunnus obesus*	Bigeye tuna	4.48 (0.93)	250	Feeds on other piscivores; tunas as top predators, SIA	(Christensen & Pauly 1998; Moteki et al. 2001; Baum & Worm 2009)	Oceanic
	T	Scombridae	*Thunnus tonggol*	Longtail tuna	4.01 (0.53)	145	Tunas as top predators	(Christensen & Pauly 1998; Moteki et al. 2001; Baum & Worm 2009)	Deep water
	E	Carcharhinidae	*Triaenodon obesus*	Whitetip reef shark	4.36 (0.75)	213	Reef sharks listed as tertiary/apex predators	(Randall 1977; Friedlander & DeMartini 2002; DeMartini et al. 2008)	Coral reef
	C	Delphinidae	*Globicephala macrorhynchus*	Short-finned pilot whale	4.3	589	Mainly cephalopods, some fish and occasionally other dolphins	(Bannister et al. 1996)	Pelagic

FG	PG	Family	Species	Common Name	TL (SE)	Max L (cm)	Justification	References	Habitat
	C	Delphinidae	*Orcaella heinsohni*	Australian snubfin dolphin	4	275	Prey on coastal and estuarine fish	Parra 2006	Inshore
	T	Gempylidae	*Ruvettus pretiosus*	Oilfish	4.18+/-0.57	200	Top predator by SIA	(Revill et al. 2009)	Pelagic
	C	Delphinidae	*Sousa chinensis*	Indo-Pacific humpbacked dolphin	4	274	Prey on coastal and estuarine fish	(Bannister et al. 1996)	Inshore
	C	Delphinidae	*Tursiops truncatus aduncus*	Bottlenose dolphin	4.2	204	Feeds on small piscivorous fish	(Dunshea 2009)	Pelagic
	C	Delphinidae	*Stenella longirostris*	Spinner dolphin	4.3	235	Feeds on small piscivorous fish	(Dolar et al. 2003)	Pelagic
	C	Ziphiidae	*Mesoplodon pacificus*	Longman's beaked whale	4.4	750	Assumed to feed on fish and squid	(Bannister et al. 1996)	Pelagic
	C	Delphinidae	*Delphinus delphis*	Short-beaked common dolphin	4.2	232	Considered a pelagic top predator	(Pusineri et al. 2008)	Pelagic
	C	Delphinidae	*Feresa attenuata*	Pygmy killer whale	4.4	207	Feeds of fish and cephalopods and probably other cetaceans	(Bannister et al. 1996)	Pelagic
	C	Delphinidae	*Steno brendanensis*	Rough-toothed dolphins	4.1	265	Feeds on cephalopods and possibly larger fish in deeper water	(Bannister et al. 1996)	Pelagic, oceanic
M	T	Lutjanidae	*Aprion virescens*	Green jobfish	3.98 (0.6)	112	Listed as apex predator	(Friedlander & DeMartini 2002)	Coral reef, pelagic
	T	Carangidae	*Carangoides fulvoguttatus*	Turrum	4.02 (0.67)	120	High proportion of teleosts in diet	(Salini et al. 1994)	Coral reef, pelagic
	T	Carangidae	*Carangoides orthogrammus*	Thicklip trevally	4.01(0.68)	50	Piscivores in diet	(Meyer et al. 2001)	Coral reef, pelagic
	T	Carangidae	*Caranx ignobilis*	Giant trevally	4.48 (0.67)	170	Estuarine piscivore, SI N Value of 11.7+/- 0.3, listed as reef apex predator, major predator of reef fishes	(Abrantes & Sheaves 2009); Dr. T. Donaldson, pers. comm..	Coral reef, pelagic
	T	Carangidae	*Caranx lugubris*	Black trevally	4.0 (0.65)	100	Feeds primarily on fish	FishBase	Coral reef, pelagic
	T	Carangidae	*Caranx melampygus*	Bluefin trevally	4.28 (0.83)	117	Listed as apex predator, diet includes piscivores	(Meyer et al. 2001; Friedlander & DeMartini 2002)	Coral reef, pelagic
	T	Carangidae	*Caranx papuensis*	Brassy trevally	4.05 (0.63)	88	Feeds primarily on fish	FishBase	Coral reef, pelagic

	T	Labridae	*Cheilinus undulatus*	Humphead Maori wrasse	3.99 (0.61)	229	Important predator on large invertebrates including crown-of-thorns starfish	(Sadovy et al. 2003), Dr. Terry Donaldson, pers. comm.	Coral reef
	T	Coryphaenidae	*Coryphaena hippurus*	Mahi mahi	4.48 (0.94)	210	Important nearshore pelagic predator of baitfishes	(Moteki et al. 2001; Revill et al. 2009), Dr. Terry Donaldson, pers. comm.	Pelagic
	T	Serranidae	*Epinephelus cyanopodus*	Purple rockcod	4.05 (0.7)	120	Feeds on some piscivores	FishBase	Coral reef, inshore
	E	Orectolobidae	*Eucrossorhinus dasypogon*	Tasselled wobbegong	3.98 (0.6)	125	Feeds on fish and invertebrates	FishBase	Coral reef
	T	Muraenidae	*Gymnothorax javanicus*	Giant moray	3.87 (0.64)	300	Important reef predator	(Randall 2005)	Coral reef
	E	Hemigaleidae	*Hemigaleus australiensis*	Australian weasel shark	~4	110	Feeds primarily on cephalopods	(Last & Stevens 2009)	Deep water
	T	Scombridae	*Katsuwonus pelamis*	Skipjack tuna	4.03 (0.64)	110	Top predator, SIA	(Kojadinovic et al. 2008)	Pelagic
	T	Lutjanidae	*Lutjanus gibbus*	Paddletail	3.63 (0.51)	50	Feeds on other piscivores, listed as tertiary predator	(Bachok et al. 2004)	Coral reef
	T	Lutjanidae	*Lutjanus monostigma*	Onespot snapper	4.27 (0.74)	60	Feeds on small fish and crustaceans	FishBase	Coral reef
	T	Lutjanidae	*Lutjanus rivulatus*	Maori snapper	4.13 (0.63)	67	Feeds on small fish and crustaceans	FishBase	Coral reef
	T	Gempylidae	*Lepidocybium flavobrunneum*	Escolar	4.34 (0.67)	200	Top predator by SIA	(Revill et al. 2009)	Deep water
	T	Lethrinidae	*Lethrinus miniatus*	Redthroat emperor	3.77 (0.58)	90	Seems to feed mainly on smaller fishes and crustaceans	FishBase	Coral reef
	T	Lutjanidae	*Lutjanus argentimaculatus*	Mangrove jack	3.85 (0.64)	150	Important predator on reefs, estuaries and rivers	(Randall 2005), Dr. T. Donaldson, pers. comm.	Coral reef, inshore
	T	Lutjanidae	*Lutjanus malabaricus*	Saddletail snapper	4.09 (0.6)	100	Feeds on other piscivores	(Bachok et al. 2004)	Coral reef
	E	Orectolobidae	*Orectolobus ornatus*	Ornate wobbegong	3.98 (0.6)	110	Feeds on fish and invertebrates	FishBase	Inshore
	E	Pseudocarcharhinidae	*Pseudocarcharias kamorahai*	Crocodile shark	4.21 (0.6)	110	Feeds on fish and cephalopods	FishBase	Pelagic
	T	Scombridae	*Scomberomorus queenslandicus*	School mackerel	4.39 (0.7)	100	Piscivores in diet	(Begg & Hopper 1997)	Nearshore pelagic

PG		Family	Species	Common Name	TL (SE)	Max L (cm)	Justification	References	Habitat
	T	Lutjanidae	*Symphorus nematophorus*	Chinamanfish	4.18 (0.71)	100	Important fish predator on coral reefs	(Randall 2005)	Coral reef
	T	Serranidae	*Variola louti*	Yellowedge coronation trout	4 (0.67)	83	Important fish predator on coral reefs	(Randall 2005)	Coral reef

Apex Predator Abundance and Distribution on the GBR

The distribution and abundance of apex predators is difficult to characterise because of their wide-ranging habits and small population sizes (Sandin & Pacala 2005). Both abiotic conditions (e.g. temperature) and prey availability are assumed to be important in determining the distribution and abundance of large predators, but predictions concerning population viability, exploitation sustainability and management requirements are still hindered by this lack of knowledge (Wirsing et al. 2007b). It is possible that long-term protected areas are the only possible benchmark available to use for ‘natural’ ecosystem states (Sandin et al. 2008), and even these may not always be representative (Robbins et al. 2006; Ayling and Choat 2008).

Much time and effort has gone into research on the distribution and abundance of selected predatory species that are of special interest and importance to GBR fisheries. Perhaps the best-known of the predator species are coral trout of the genus *Plectropomus* (Choat & Russell 2008). Less is known about large sharks (Chin & Kyne 2007), and very little is known about wide-ranging pelagic species such as cetaceans, mackerel, billfish, carangids (trevallies) or barracuda.

Although some effort has gone into quantifying the distribution and abundance of predators in reef habitats, there is also evidence for the use of non-reef environments by reef predators, especially during reproductively active or juvenile stages (Adams et al. 2006). For instance, mainland estuaries inshore of the GBR are important nursery areas for the mangrove jack *Lutjanus argentimaculatus* and the groupers *Epinephelus coioides* and *E. malabaricus* (Sheaves 1995). More mobile and wide-ranging species, such as the giant trevally *Caranx ignobilis*, are known to use back-reef ecosystems as juveniles, before moving to deeper habitats as adults (Wetherbee et al. 2004).

By combining data from the AIMS Long Term Monitoring Program, information from the Effects of Line Fishing (ELF) experiment (e.g. Mapstone et al. 2008), data collected by the authors, shark abundance estimates off Townsville, shark control program catches, and fisheries catch data; the 115 predator species were ranked in order of abundance. It is important to note that the abundance rankings are relative measures. The resulting ranking shows that the smaller generalist top predators are more abundant than higher-level apex predators, often by several orders of magnitude (Table 3). Of the apex predators, the tiger shark and bull shark rank highest, followed by pelagic and inshore species. Coral trout, red bass and a number of pelagic species are ranked as the most abundant generalist top predators, while smaller snappers and trevallies emerge as the most abundant high-level mesopredators. Many predators are rare on the GBR (ranks of 10 or less) including 18 apex predators (78.2%), 34 generalist top predators (50.7%) and 9 high-level mesopredators (33.3%). Not surprisingly, the higher trophic categories have greater proportions of rare species.

Table 3. Relative abundance ranking for all GBR predator species considered in this review. Higher rankings reflect greater relative abundance. Functional groups (FG) are A: apex predators; G: generalist top predators and H: high-level mesopredators. For calculation of abundance categories, refer to methods section, page 16.

FG	Species	Common name	Abundance category
A	*Galeocerdo cuvier*	Tiger shark	95
	Carcharhinus leucas	Bull shark	70
	Xiphias gladius	Swordfish	40
	Sphyrna leweni	Scalloped hammerhead	35
	Carcharhinus amboinensis	Pigeye shark	10
	Sphyrna mokarran	Great hammerhead	8

FG	Species	Common name	Abundance category
	Tetrapturus audax	Striped marlin	8
	Negaprion acutidens	Lemon shark	4
	Carcharhinus albimarginatus	Silvertip shark	3
	Crocodylus porosus	Estuarine crocodile	3
	Carcharhinus falciformis	Silky shark	2
	Carcharhinus obscurus	Dusky shark	2
	Isurus oxyrhinchus	Shortfin mako	2
	Carcharhinus altimus	Bignose shark	1
	Carcharhinus longimanus	Oceanic whitetip shark	1
	Carcharias taurus	Greynurse shark	1
	Carcharodon carcharias	White shark	1
	Isurus paucus	Longfin mako	1
	Makaira indica	Black marlin	1
	Makaira mazara	Indo-Pacific blue marlin	1
	Orcinus orca	Orca	1
	Pseudorca crassidens	False killer whale	1
G	*Plectropomus leopardus*	Common coral trout	5300
	Euthynnus affinis	Mackerel tuna	1200
	Lutjans bohar	Red bass	625
	Thunnus alalunga	Albacore	350
	Plectropomus laevis	Bluespotted coral trout	260
	Plectropomus maculatus	Barcheek coral trout	164
	Sphyraena jello	Pickhandle barracuda	150
	Sphyraena qenie	Blackfin barracuda	150
	Thunnus albacares	Yellowfin tuna	120
	Scomberomorus semifasciatus	Grey mackerel	100
	Triaenodon obesus	Whitetip reef shark	95
	Sphyraena barracuda	Great barracuda	70
	Carcharhinus tilstoni	Australian blacktip shark	45
	Epinephelus polyphekadion	Camouflage grouper	45
	Carcharhinus amblyrhinchos	Grey reef shark	40
	Carcharhinus sorrah	Spot-tail shark	40
	Thunnus obesus	Bigeye tuna	40
	Centrophorus moluccensis	Endeavour dogfish	30
	Centrophorus niaukang	Taiwan gulper shark	30
	Dalatias licha	Black shark	30
	Heptranchias perlo	Sharpnose sevengill shark	30
	Squalus montalbani	Philippine spurdog	30
	Stenella longirostris	Spinner dolphin	30
	Epinephelus fuscoguttatus	Flowery rockcod	26
	Carcharhinus limbatus	Common blacktip shark	25
	Carcharhinus melanopterus	Blacktip reef shark	25
	Carcharhinus dussumieri	Whitecheek shark	20
	Eusphyra blochii	Winghead shark	20
	Rhizoprionodon acutus	Milk shark	20
	Squalus megalops	Spiked spurdog	20

FG	Species	Common name	Abundance category
	Carcharhinus brevipinna	Spinner shark	15
	Rhizoprionodon taylori	Australian sharpnose shark	15
	Sousa chinensis	Indo-Pacific humpbacked dolphin	15
	Tursiops truncatus aduncus	Bottlenose dolphin	10
	Scomberomorus commerson	Spanish mackerel	6
	Acanthocybium solandri	Wahoo	5
	Carcharhinus cautus	Nervous shark	5
	Carcharhinus macloti	Hardnose shark	5
	Delphinus delphis	Short-beaked common dolphin	5
	Hemipristis elongata	Fossil shark	5
	Hexanchus makanurai	Bigeye sixgill shark	5
	Hypogaleus hyugaensis	Pencil shark	5
	Orcaella heinsohni	Australian snubfin dolphin	5
	Prionace glauca	Blue shark	5
	Plectropomus areolatus	Passionfruit coral trout	4
	Carcharhinus fitzroyensis	Creek whaler	3
	Gempylus serpens	Snake mackerel	3
	Tetrapturus angustirostris	Shortbill spearfish	3
	Carcharhinus plumbeus	Sandbar shark	2
	Epinephelus coioides	Goldspotted rockcod	2
	Alopias superciliosus	Bigeye thresher	1
	Carcharhinus amblyrhynchoides	Graceful shark	1
	Echinorhinus cookii	Prickly shark	1
	Epinephelus lanceolatus	Queensland groper	1
	Epinephelus malabaricus	Blackspotted rockcod	1
	Epinephelus tukula	Potato rockcod	1
	Feresa attenuata	Pygmy killer whale	1
	Globicephala macrorhynchus	Short-finned pilot whale	1
	Globicephala melas	Long-finned pilot whale	1
	Glyphis glyphis	Speartooth shark	1
	Gymnosarda unicolor	Dogtooth tuna	1
	Istiophorus platypterus	Sailfish	1
	Mesoplodon pacificus	Longman's beaked whale	1
	Orectolobus maculatus	Spotted wobbegong	1
	Steno brendanensis	Rough-toothed dolphins	1
	Thunnus tonggol	Longtail tuna	1
	Ruvettus pretiosus	Oilfish	1
H	*Lutjanus gibbus*	Paddletail	780
	Lethrinus miniatus	Redthroat emperor	760
	Carangoides fulvoguttatus	Turrum	200
	Scomberomorus queenslandicus	School mackerel	200
	Cheilinus undulatus	Humphead Maori wrasse	105
	Caranx melampygus	Bluefin trevally	80
	Symphorus nematophorus	Chinamanfish	60

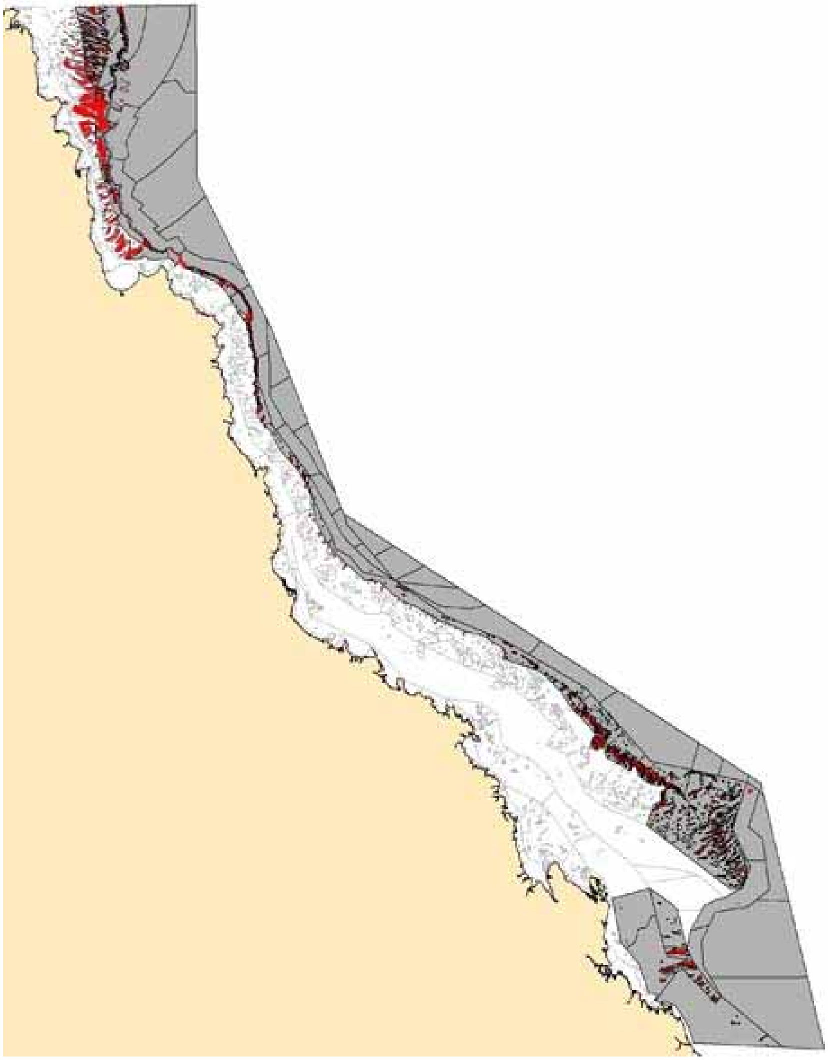
FG	Species	Common name	Abundance category
	Caranx ignobilis	Giant trevally	50
	Lutjanus malabaricus	Saddletail snapper	50
	Lutjanus monostigma	Onespot snapper	40
	Aprion virescens	Green jobfish	20
	Coryphaena hippurus	Mahi mahi	20
	Lepidocybium flavobrunneum	Escolar	20
	Lutjanus argentimaculatus	Mangrove jack	20
	Variola louti	Yellowedge coronation trout	18
	Katsuwonus pelamis	Skipjack tuna	15
	Epinephelus cyanopodus	Purple rockcod	13
	Orectolobus ornatus	Ornate wobbegong	10
	Gymnothorax javanicus	Giant moray	10
	Lutjanus rivulatus	Maori snapper	6
	Carangoides orthogrammus	Thicklip trevally	5
	Eucrossorhinus dasypogon	Tasselled wobbegong	5
	Caranx lugubris	Black trevally	1
	Caranx papuensis	Brassy trevally	1
	Hemigaleus australiensis	Australian weasel shark	1
	Pseudocarcharias kamoharai	Crocodile shark	1

Individual Species Profiles

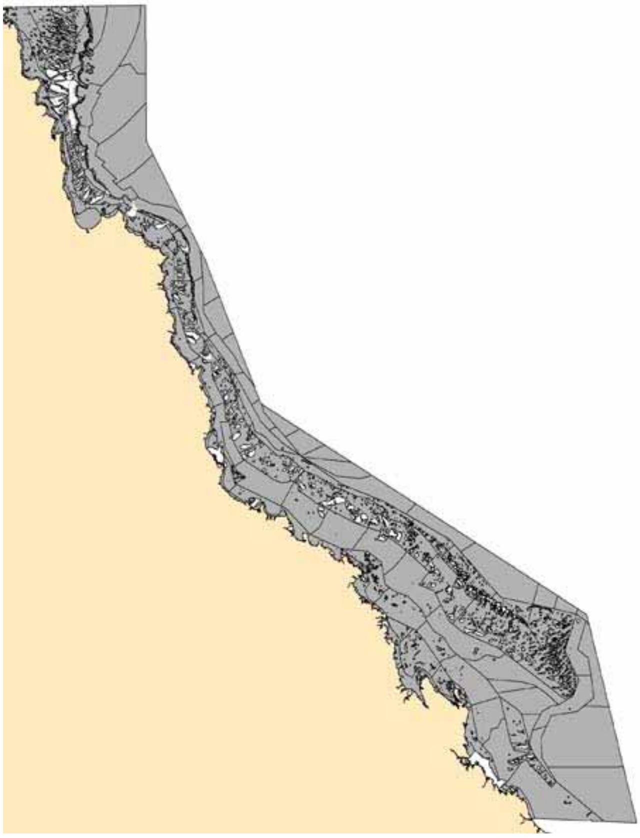
***Carcharhinus albimarginatus* (Silvertip shark)**

Maximum length: 275cm	Maximum age: Unknown
Length at maturity: M: 170cm; F: 195cm	Age at maturity: Unknown, but probably around 20 yrs
Distribution and abundance: Likely to occur along the entire length of the outer GBR. Most abundant on the front of outer shelf reefs but also occurs occasionally around mid shelf reefs and can be found in open water some distance from reefs. Abundance: Very variable but in preferred habitats has an estimated density ranking of 3 individuals per 100 ha.	Feeding: Feeds on a variety of pelagic and demersal fishes, including other elasmobranchs.
Reproduction: Viviparous. Produces 6-11 pups after a gestation period of 12 months. Born at 70-80cm length.	Other information: Tagging studies have suggested silvertips are relatively site-attached, staying within 2 km of the initial capture site.

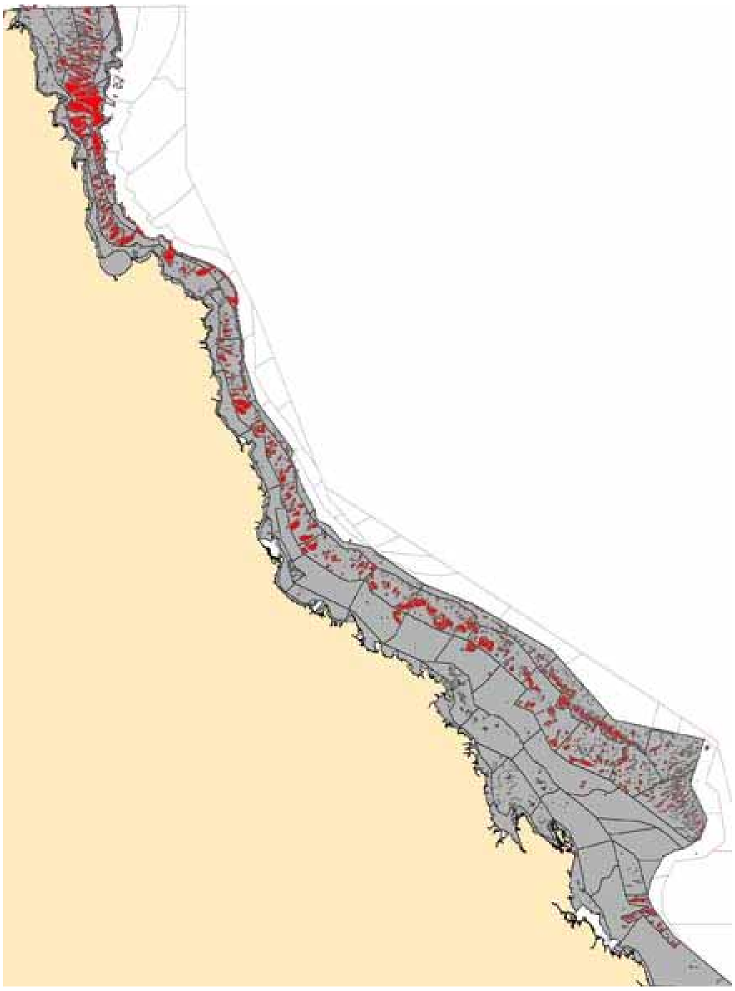
Likely bioregional distribution (indicated by grey non-reef and red reef bioregions):



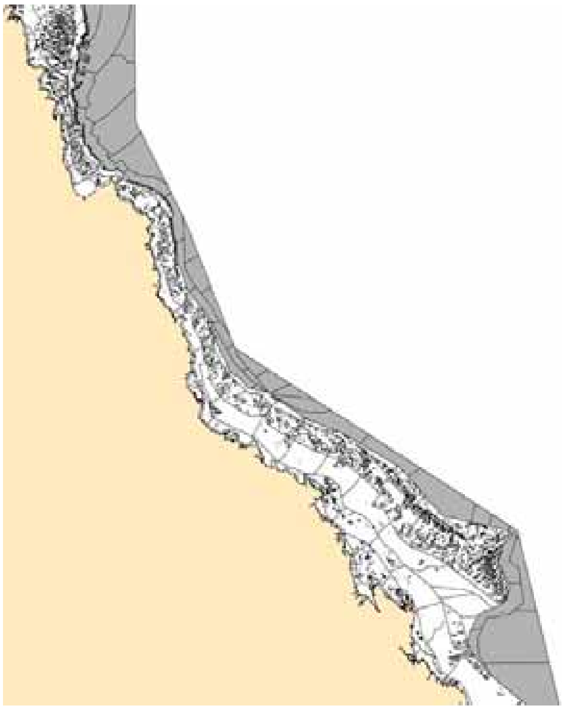
Carcharhinus altimus (Bignose shark)

<table>
<tr><td>Maximum length: 300cm Maximum</td><td>age: Unknown</td></tr>
<tr><td>Length at maturity: M: 195cm; F: 225cm</td><td>Age at maturity: Unknown</td></tr>
<tr><td>Distribution and abundance: Deep-benthic species that undetakes nocturnal migrations into shallower pelagic habitats. In north-eastern Australia it is thought to occur on the continental shelf in depths of between 90 and 500m (Anderson & Stevens 1996). Likely to occur along the entire length of the outer GBR.
Abundance: Not often caught, have a density ranking of less than 1 individual per 100 ha.</td><td>Feeding: Feeds on bony fishes, other sharks, stingrays, and cuttlefish. A high proportion of prey consists of demersal species.</td></tr>
<tr><td>Reproduction: Viviparous, litter sizes range from 3 to 15, the gestation period is unknown, and the size at birth is reported to be between 70 and 90 cm TL (Stevens & McLoughlin 1991).</td><td>Other information: Very little information is available about this shark. It is occasionally caught in offshore pelagic longlines, and has been caught in the inshore shark control program. A tagging study found that an individual travelled a maximum distance of 3,343km over 11 years (Kohler & Turner 2001).</td></tr>
<tr><td colspan="2">Likely bioregional distribution (all (grey) non-reef bioregions):
</td></tr>
</table>

Carcharhinus amboinensis (Pigeye shark)

Maximum length: 280cm	**Maximum age:** Probably around 30y
Length at maturity: M: 210cm; F: 215cm	**Age at maturity:** Unknown
Distribution and abundance: Widely distributed around reefs and in inter-reefal areas. Abundance: Usually uncommon around offshore reefs with an estimated density ranking of 10 per 100 ha but easily confused with bull shark.	**Feeding:** Similar to the bull shark. Feeds mainly on bottom-living bony fishes, other sharks, rays, crustaceans, cephalopods and other molluscs.
Reproduction: Viviparous. Gives birth to litters 6-13 young after a 12-month gestation.	**Other information:** Looks very similar to the bull shark and often confused with that species. Tagging studies show movements of 240-1,080 km from the tagging site.
Likely bioregional distribution (indicated by grey non-reef and red reef bioregions): 	

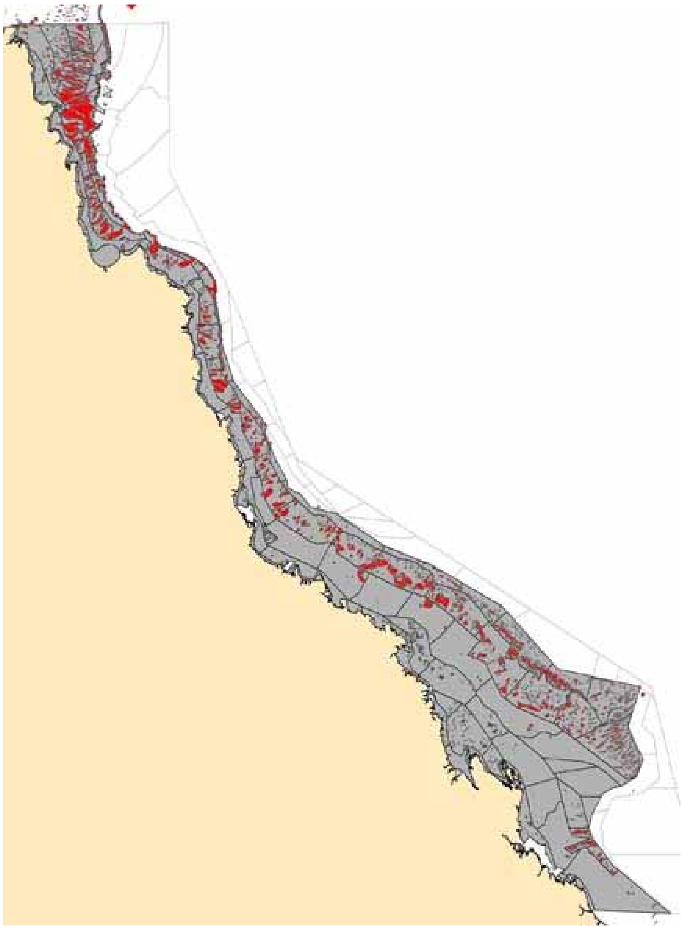
Carcharhinus falciformis (Silky shark)

Maximum length: 350cm	**Maximum age:** 25y
Length at maturity: Males from the east coast of Australia mature at 210-215 cm, and females at about 200 cm TL (Stevens & McLoughlin 1991).	**Age at maturity:** 6-10y
Distribution and abundance: On the edge of the continental shelf and in the open ocean from the surface to at least 500 m depth; occasionally recorded in inshore areas as shallow as 18 m. Abundance: Unknown but is present in oceanic waters with an estimated density ranking of 2 individuals per 100 ha.	**Feeding:** Feeds primarily on fish and is often found with schools of tuna. Was found to be among the top-level predators in the pelagic environment (Revill et al. 2009).
Reproduction: Viviparous. *C. falciformis* from the east coast of Australia shows no reproductive seasonality. Litter sizes range from 5 to 8 with a mean of 7, the gestation period is unknown, and the size at birth is about 70-85 cm TL (Stevens & McLoughlin 1991).	**Other information:** A tagging study found that an individual travelled a maximum distance of 1,339km over 7 years (Kohler & Turner 2001). Fishing mortality required to drive this species to extinction was calculated to be at the low end of the scale, indicating high vulnerability to extinction (Garcia et al. 2008). One of the most abundant sharks caught in Indonesian fisheries, both in terms of abundance and biomass (White 2007). Accounted for 3% of sportfishing catch in NSW (Stevens 1984).
Likely bioregional distribution (all offshore pelagic bioregions): 	

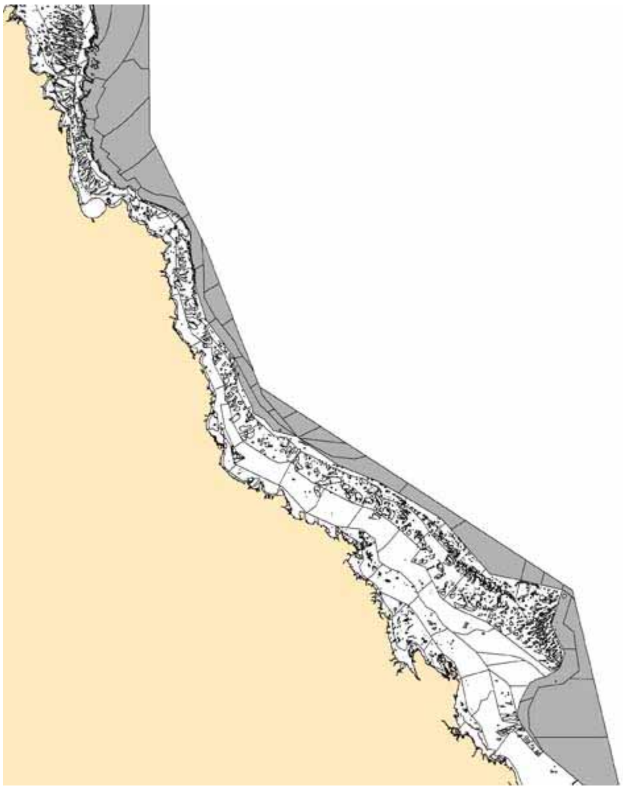
Carcharhinus leucas (Bull shark)

Maximum length: 350cm	**Maximum age:** 32y
Length at maturity: M: 160-200cm; F: 180-230cm	**Age at maturity:** 10-15y
Distribution and abundance:. Inhabits shallow coastal and estuarine waters. Can be found in near-freshwater conditions and also on offshore coral reefs. Abundance: Relatively common in estuaries and inshore areas: estimated density ranking of 70 per 100 ha but rare on the reef	**Feeding:** A highly adaptable predator that starts taking large prey at a relatively small size, and is a known predator of dolphins (Heithaus 2001a). Feeds on bony fishes, other sharks, rays, mantis shrimps, crabs, squid, sea snails, sea urchins, mammalian carrion, sea turtles, and occasionally garbage.
Reproduction: Viviparous. Gives birth to litters of up to 13 young after an 11-month gestation.	**Other information:** Can endure an extremely wide range of salinity levels (Pillans et al. 2008; Ortega et al. 2009). Variations in salinity and dissolved oxygen can affect the distribution of juvenile and adult sharks (Heupel & Simpfendorfer 2008), and therefore affect their effects on prey species (Heithaus et al. 2009).

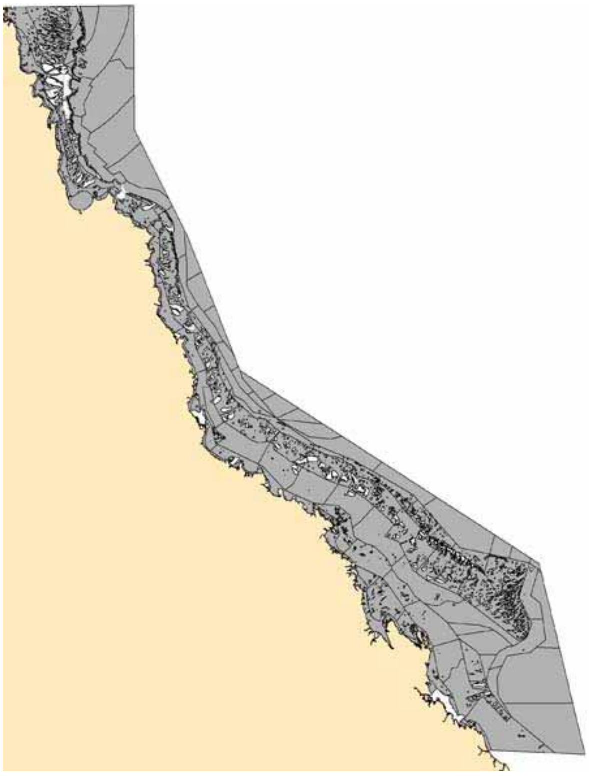
Likely bioregional distribution (indicated by grey non-reef and red reef bioregions):



Carcharhinus longimanus (Oceanic whitetip shark)

Maximum length: 350cm	**Maximum age:** 22y
Length at maturity: 180-200cm	**Age at maturity:** 6-7y
Distribution and abundance: An oceanic species occasionally occurring over the continental shelf, especially where the shelf is narrow (Lessa et al. 1999). Abundance: Unknown has an estimated density ranking of 1 individual per 100 ha in the oceanic GBR region	**Feeding:** Feeds on pelagic fish (eg. tuna and mahimahi), threadfins, stingrays, sea turtles, seabirds, gastropods, squid, crustaceans, mammalian carrion, cetaceans (Heithaus 2001a) and garbage.
Reproduction: Viviparous, placental, Litter size 1-15; 60-65 cm	**Other information:** A tagging study found that an individual travelled a maximum distance of 2,811km over 3 years (Kohler & Turner 2001). Common longline by-catch species, often second only to the blue shark *Prionace glauca* (Stevens & Wayte 1998; Lessa et al. 1999), and was found to make up 4% of the sportfishing catch off NSW (Stevens 1984). Fishing mortality required to drive this species to extinction was calculated to be at the low end of the scale, indicating high vulnerability to extinction (Garcia et al. 2008).
Likely bioregional distribution (all offshore pelagic bioregions): 	

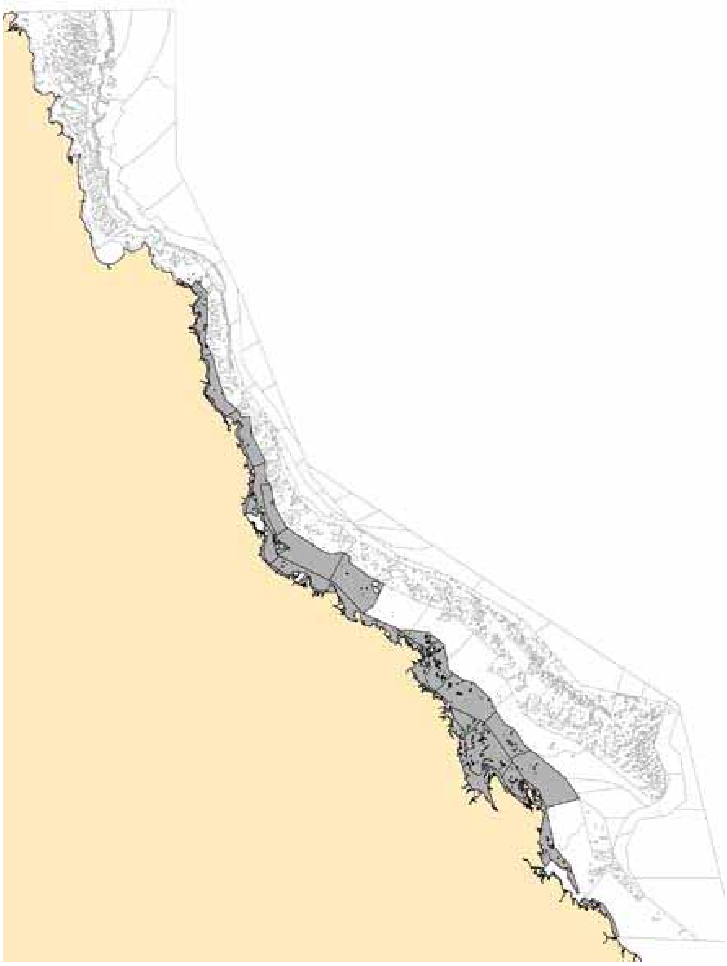
Carcharhinus obscurus (Dusky shark)

Maximum length: 420cm	**Maximum age:** 40y
Length at maturity: 280cm	**Age at maturity:** 20y
Distribution and abundance: Found in offshore and coastal waters over the continental shelf, probably migrate north and into deeper water as they age. Abundance: Unknown due to confusion with other species (e.g. bronze whaler *C. brachyurus*), estimated density ranking of 2 individuals per 100 in the GBR region.	**Feeding:** Feed on fish, smaller sharks – can be cannibalistic (Stevens 1984), cephalopods and crustaceans, sometimes mammalian carrion and can ingest inorganic objects. A common predator of cetaceans (Heithaus 2001a)
Reproduction: Viviparous, yolk-sac placenta, litter size 3-14; 70-100 cm, gestation ~ 16 months	**Other information:** Described as one of the most K-selected of all shark species (Simpfendorfer et al. 2002b; Garcia et al. 2008). Although preliminary analysis deemed exploitation rates to be sustainable, a declining trend in WA catch rates has been recently reported despite a 22% effort reduction in the targeted fishery (McAuley et al. 2007). A tagging study found that most small sharks stay within 100km, but seasonal migrations of over 1,300km can occur (Hussey et al. 2009).
Likely bioregional distribution (all non-reef bioregions): 	

Carcharias taurus (Greynurse shark)

Maximum length: 320cm	**Maximum age:** 25+y
Length at maturity: 220cm	**Age at maturity:** 6-8y
Distribution and abundance: Commonly found on inshore rocky or coral reefs. In Australia found primarily in NSW and southern Queensland; their range is likely to only just extend into the southern GBRMP (Otway et al. 2004). Abundance: Unknown but probably rare in the GBR region with an estimated density ranking of less than 1 per 100 ha.	**Feeding:** Feed on fish and other sharks and rays (e.g. *C. obscurus*), cephalopods and crustaceans.
Reproduction: Ovoviviparous, producing 2 young every second year, gestation 9-12 months.	**Other information:** Listed as Vulnerable on the IUCN Red List, and is one of the sharks most seriously threatened with extinction (Garcia et al. 2008). A tagging study found that an individual travelled a maximum distance of 1,897km over 11 years (Kohler & Turner 2001).

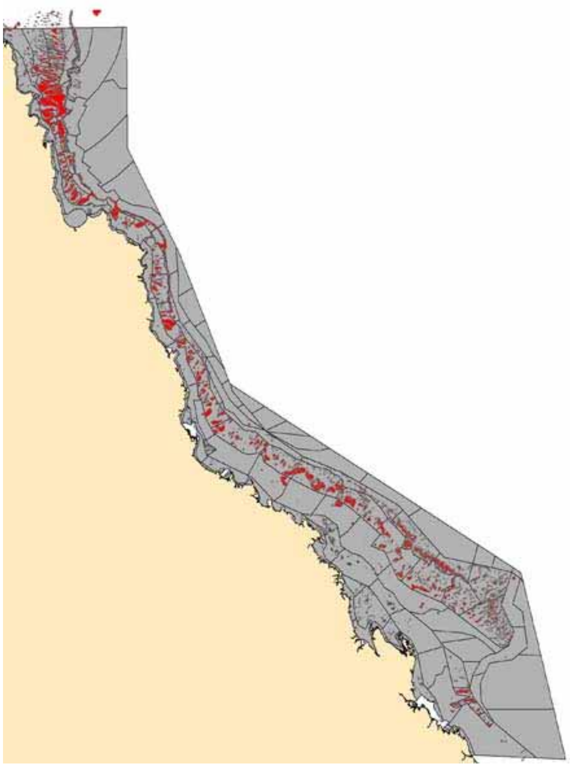
Likely bioregional distribution (indicated by grey non-reef bioregions):



Carcharodon carcharias (White shark)

Maximum length: 600cm	**Maximum age:** 60y
Length at maturity: male: 350-400cm, female: 400-500cm	**Age at maturity:** 12-17y
Distribution and abundance: Occurs in coastal, offshore and pelagic environments. Can migrate large distances. Normally found in temperate regions but has been observed in tropical waters; a tagging study followed an individual to waters off Rockhampton (Bruce et al. 2006). Abundance: Unknown but probably rare in the GBR region with an estimated density ranking of less than 1 per 100 ha.	**Feeding:** Feeds on fish, sharks, rays, seals, cetaceans, seabirds, carrion, squid, octopi and crabs. Considered the world's largest predator.
Reproduction: Ovoviviparous, with 2-17 young per litter, 130cm. Females possibly give birth to only 80 pups during their lifetime.	**Other information:** Listed as Vulnerable on the IUCN Red List, and is one of the sharks most seriously threatened with extinction (Walker 1998; Garcia et al. 2008). Can undertake long migrations; a tagging study recaptured an individual in New Zealand, some 3,550 km from the point of tagging in South Australia (Bruce et al. 2006). One female satellite tagged in South Africa swam to Western Australia and back to the tagging site, travelling 22,000 km in 10 months.

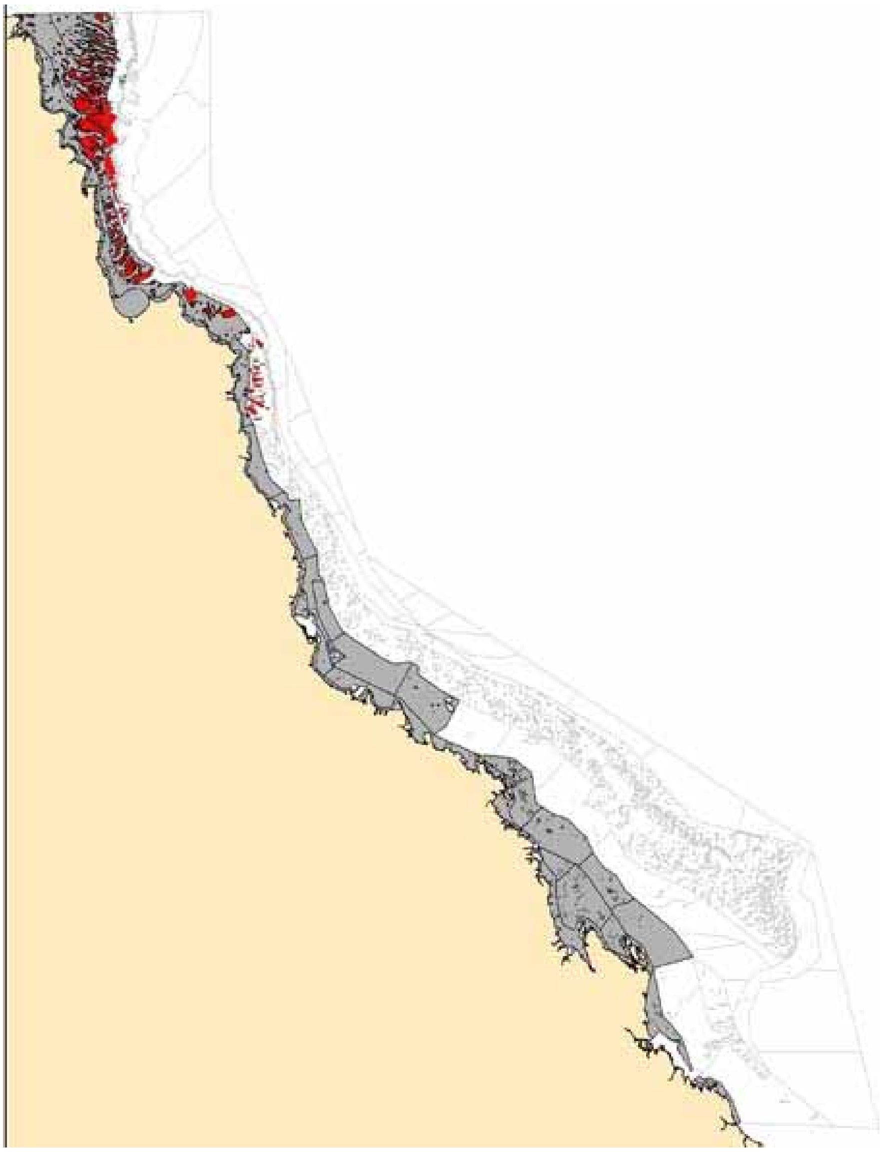
Likely bioregional distribution (indicated by grey non-reef and red reef bioregions):



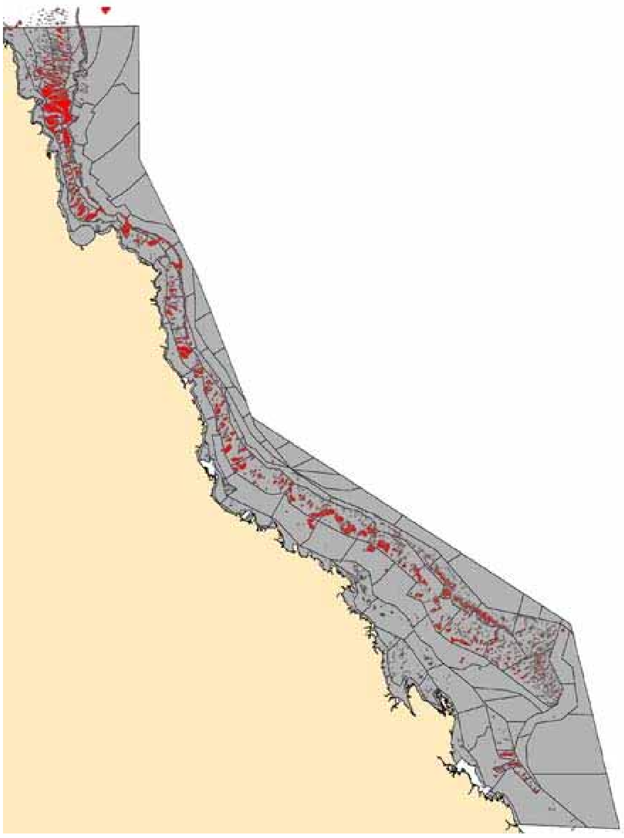
Crocodylus porosus (Estuarine crocodile)

Maximum length: 600cm	**Maximum age:** Unknown
Length at maturity: Unknown	**Age at maturity:** M: 16y; F: 10-12y
Distribution and abundance: Estuaries and turbid coastal habitats, although sightings have occurred in offshore areas including northern outer barrier reefs. Density on GBRMP coast recorded at 0.2-2.7 individuals per km. Estimated density ranking of 3 per 100 ha.	**Feeding:** Opportunistic apex predator; feed on sharks, fish, carrion, mammals and invertebrates.
Reproduction: Mound nesting, 60-80 eggs guarded for 3 months. Sex determination by nest temperature.	**Other information:** Were hunted to near extinction but have recovered strongly in Australia after 30 years of protection. Variations in crocodile density most likely attributable to environmental differences (Fukuda et al. 2007).

Likely bioregional distribution (indicated by grey non-reef and red reef bioregions):



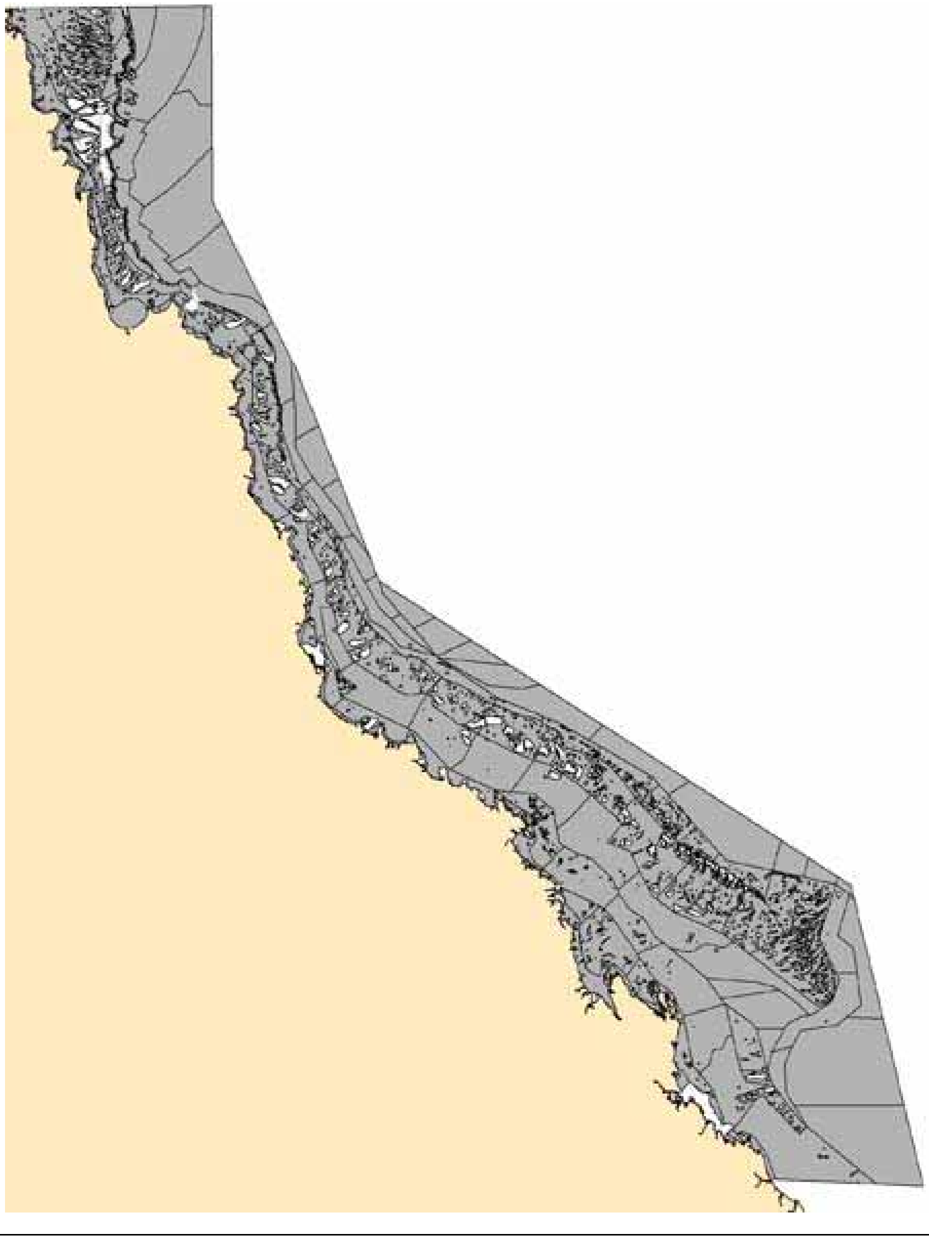
Galeocerdo cuvier (Tiger shark)

<table>
<tr><td>Maximum length: 600cm</td><td>Maximum age: 50y</td></tr>
<tr><td>Length at maturity: M: ~292cm; F: 330-345cm</td><td>Age at maturity: 10y</td></tr>
<tr><td>Distribution and abundance: Found across all GBR habitats, including reefs, inshore areas and offshore pelagic habitats.
Abundance: Relatively common with an estimated density ranking of 95 individuals per 100 ha.</td><td>Feeding: Common predator of fish, sharks, cetaceans, dugongs and marine turtles. Ontogenetic shift in diet, with more pelagic prey taken later in life (Heithaus 2001b). they are attracted to large aggregations of vertebrate prey (eg. turtle nesting sites) (Dill et al. 2003; Heithaus et al. 2008b).</td></tr>
<tr><td>Reproduction: Ovoviviparous, give birth every 2 years to 10-80 young of 80-90cm, gestation 15-16 months (Whitney & Crow 2007).</td><td>Other information: One of the strongest swimmers of the carcharhinid family (Heithaus 2001b). Has been subject to a number of studies in Shark Bay, Western Australia, where it exerts a strong top-down control of the abundance and behaviour of prey and competitors, including dolphins, turtles and seabirds (Heithaus & Dill 2006). Can undertake lengthy migration, with movements of up to 8,000km recorded in a single tagged individual (Heithaus et al. 2007b).</td></tr>
<tr><td colspan="2">Likely bioregional distribution (indicated by grey non-reef and red reef bioregions):
</td></tr>
</table>

Istiophorus platypterus (sailfish)

Maximum length: 350cm	**Maximum age:** 13y
Length at maturity: Unknown	**Age at maturity:** Unknown
Distribution and abundance: Oceanic, usually found above the thermocline. Estimated density ranking of 1 individual per 100 ha.	**Feeding:** Feeds mainly on fishes, crustaceans and cephalopods. Prey is primarily pelagic (Rosas-Alayola et al. 2002).
Reproduction: Likely to spawn throughout the year in tropical and subtropical waters of the Pacific, with peak spawning in summer.	**Other information:** There is a great lack of knowledge on billfish life histories and movement patterns. The NSW tagging recovery rate for all billfish was 0.75% between 1973 and 2003 (Ortiz et al. 2003).

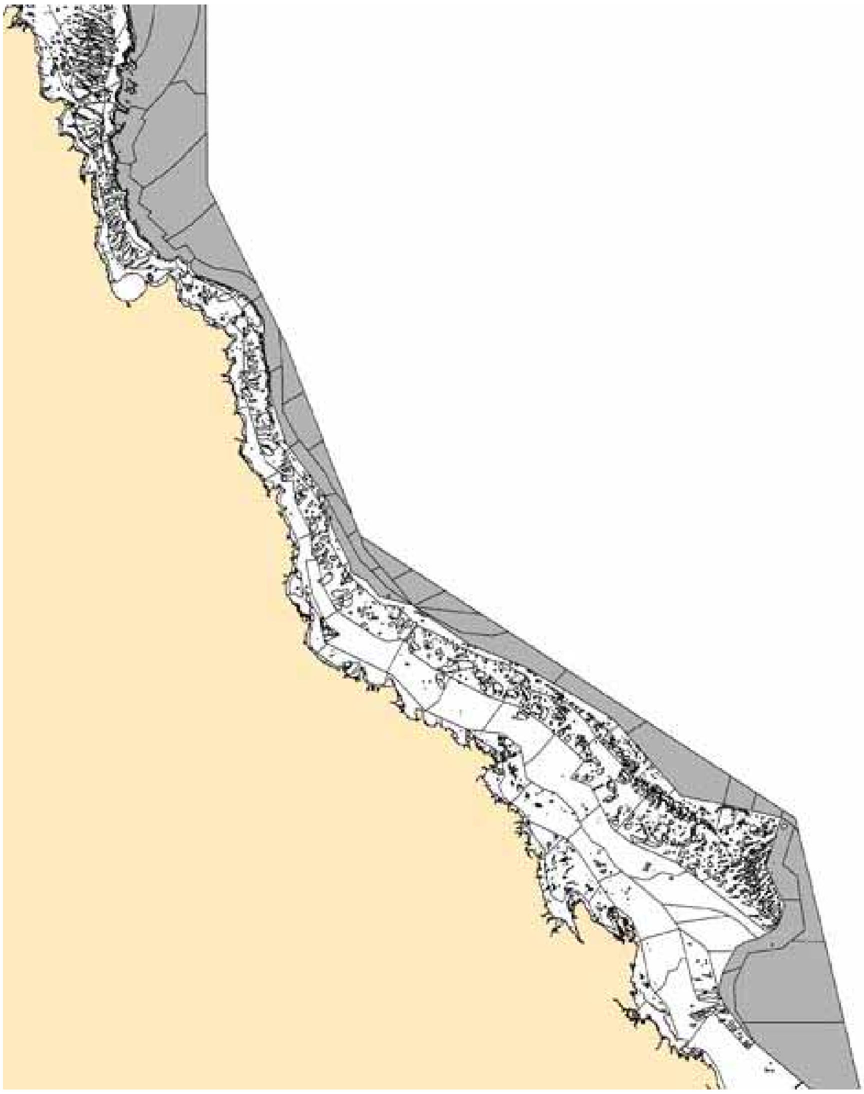
Likely bioregional distribution (all non-reef bioregions):



Isurus oxyrhynchus (Shortfin mako)

Maximum length: 400cm	**Maximum age:** 25y
Length at maturity: M: 195cm; F: 280cm	**Age at maturity:** M: 8y; F:18y
Distribution and abundance: Oceanic, usually in surface waters. Abundance: Unknown, probably rare in the GBR region with an estimated density ranking of less than 1 per 100 ha.	**Feeding:** Feed on fish, sharks and cephalopods, occasionally marine mammals (Heithaus 2001a). Are considered apex predators in the pelagic food chain (Revill et al. 2009).
Reproduction: Viviparous, 4-16 young of 60-70cm every three years, gestation period 15-18 months.	**Other information:** Fastest-swimming shark, occasionally caught in longlines (Stevens & Wayte 1998). Also caught by sportfishers in winter months (Stevens 1984).

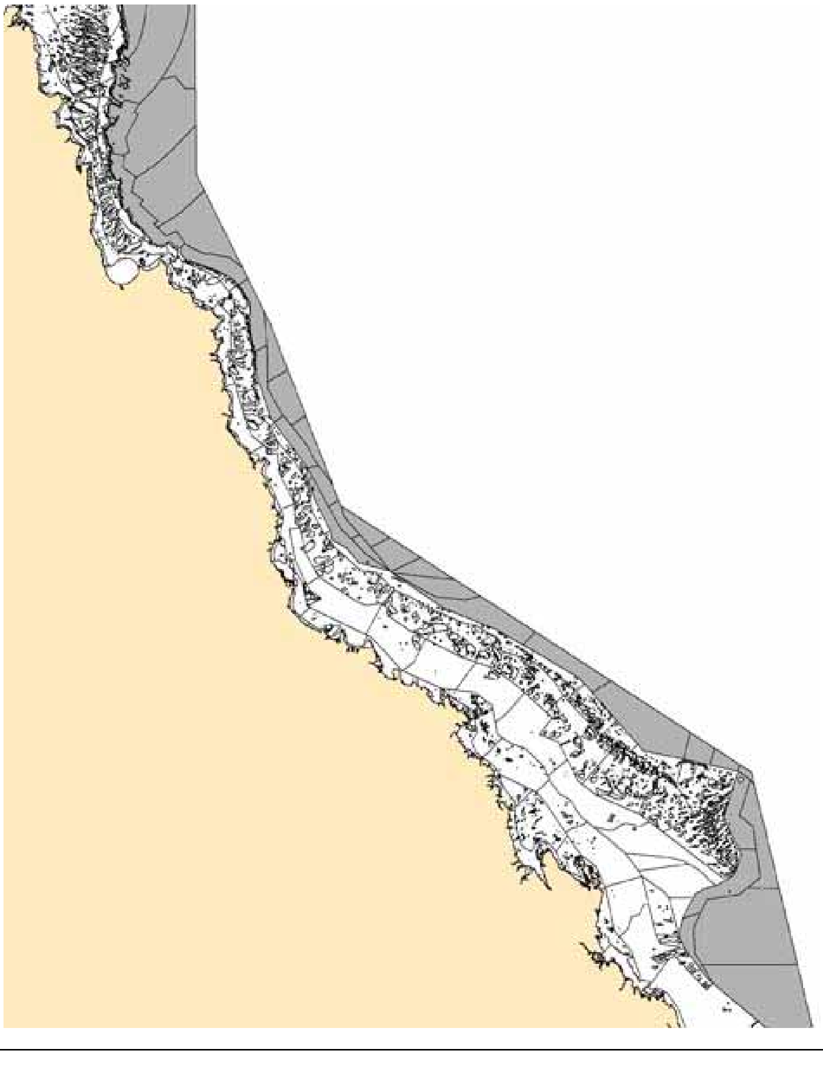
Likely bioregional distribution (all offshore pelagic bioregions):



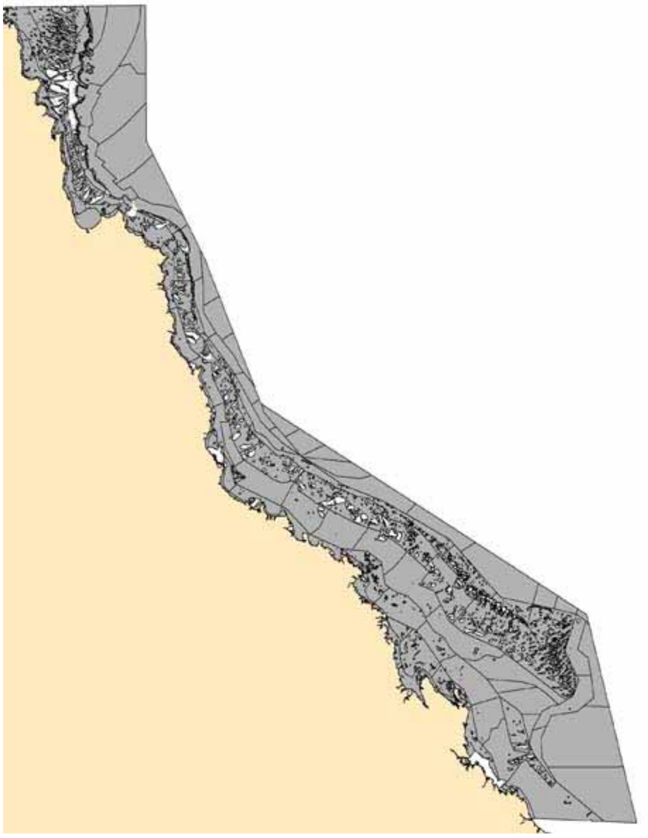
Isurus paucus (Longfin mako)

Maximum length: 417cm	**Maximum age:** Unknown
Length at maturity: M: 205-228cm; F: 245cm	**Age at maturity:** Unknown
Distribution and abundance: Oceanic and pelagic, possibly in deeper water than the shortfin mako (Last & Stevens 2009). Abundance: Unknown due to confusion with the shortfin mako, estimated density ranking of less than 1 individual per 100 ha.	**Feeding:** Feed on pelagic fishes and cephalopods (Last & Stevens 2009).
Reproduction: Oophagous, 2-8 young of 95-120cm.	**Other information:** Probably slower swimming that its short-finned relative, occasionally caught in longlines (Stevens & Wayte 1998).

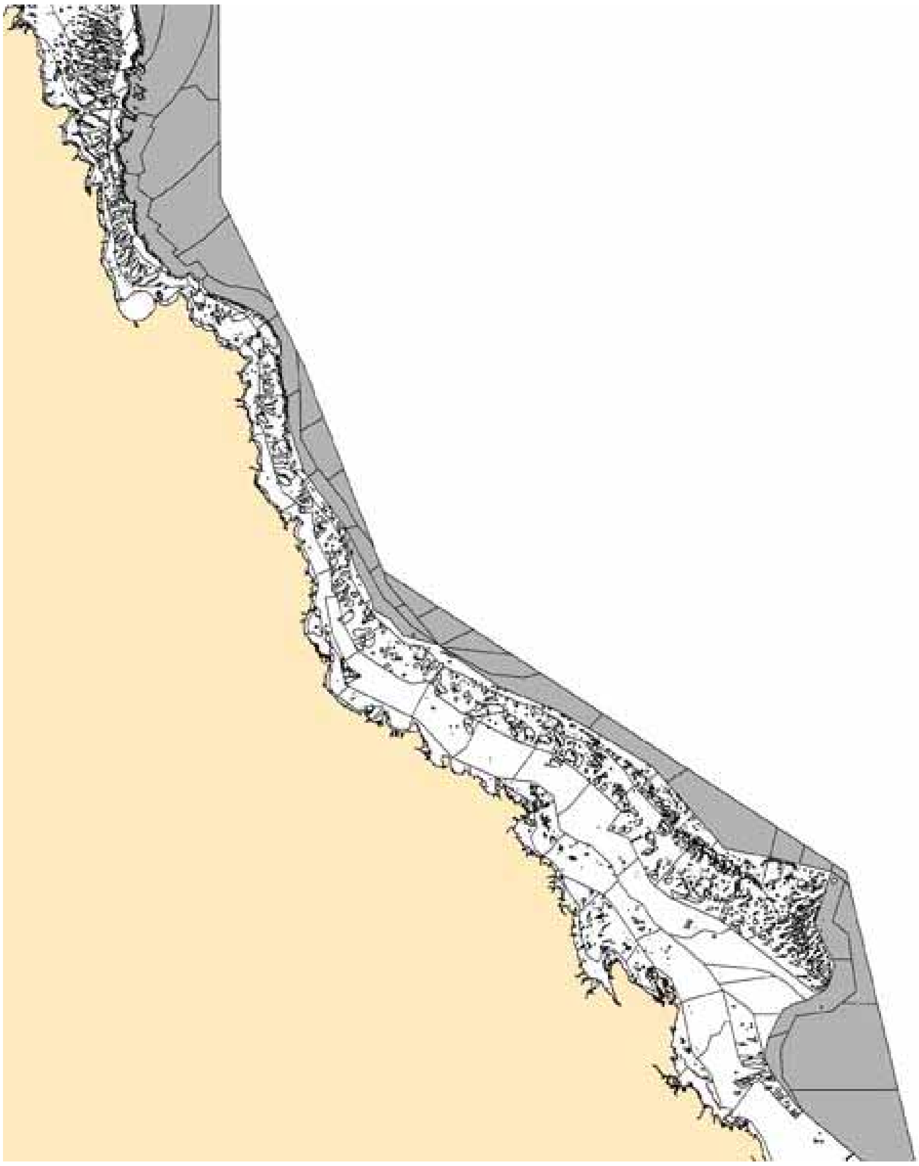
Likely bioregional distribution (all offshore pelagic bioregions):



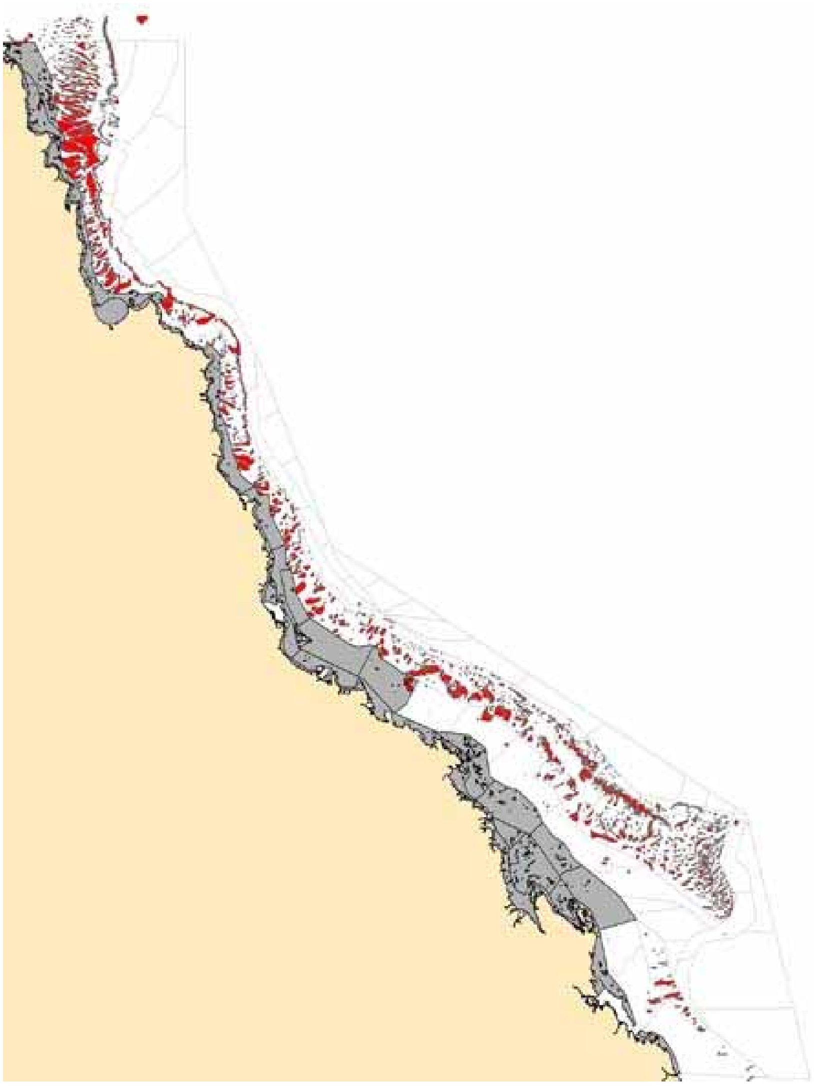
Makaira indica (Black marlin)

Maximum length: 465cm	**Maximum age:** Unknown
Length at maturity: Unknown	**Age at maturity:** Unknown
Distribution and abundance: Oceanic, usually in surface waters. Estimated density ranking of 1 individual per 100 ha.	**Feeding:** Feed on fish (especially tunas), cephalopods and crustaceans (Bachok et al. 2004).
Reproduction: Commonly spawns in warm waters.	**Other information:** The north-west Coral Sea supports a seasonally high density of black marlin, believed to be a major spawning aggregation between September and December. The world's premier black marlin sportfishing event is held here, between Cairns and Lizard Island, each year (Speare 2003). Between 1972 and 1999, over 20,000 black marlin were tagged and released inside and outside the GBR by the sport fishery, and 190 (0.95%) have been recaptured (Pepperell & Davis 1999). Most of the large fish caught are gravid femailes, and the effect of the capture and release on the capacity to reproduce is unknown. Anecdotal evidence suggests that shark attacks on hooked black marlin are relatively common (Pepperell & Davis 1999).
Likely bioregional distribution (all non-reef bioregions): 	

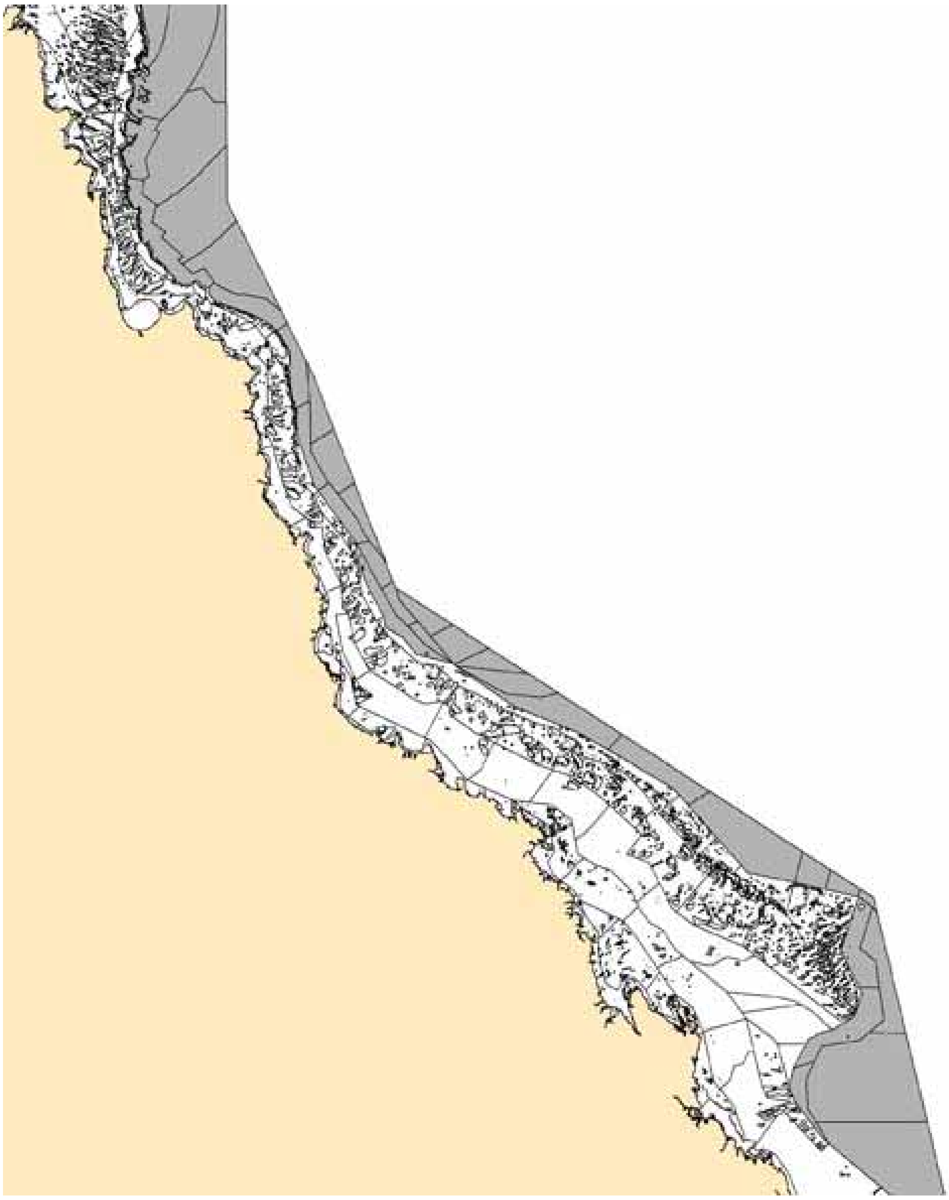
Makaira mazara (IndoPacific blue marlin)

Maximum length: 500cm	**Maximum age:** 28y
Length at maturity: Unknown	**Age at maturity:** Unknown
Distribution and abundance: Oceanic, usually in surface waters. Estimated density ranking of 1 individual per 100 ha.	**Feeding:** Feed on squids, tuna-like fishes, crustaceans and cephalopods (Abitia-Cardenas et al. 1999).
Reproduction: Spawning during summer in equatorial waters to 30° latitude, in both the Indian and Pacific oceans.	**Other information:**
Likely bioregional distribution (all offshore pelagic bioregions): 	

Negaprion acutidens (Lemon shark)

Maximum length: 300cm	**Maximum age:** Probably about 30 years
Length at maturity: 220cm	**Age at maturity:** Unknown
Distribution and abundance: Often found in very shallow water in lagoons, mangroves or on reef flats, sometimes in estuaries especially as juveniles (Salini et al. 1992). Prefers unvegetated inshore environments as nursery areas (White & Potter 2004). Abundance: Relatively rare with an estimated density ranking of 4 per 100 ha.	**Feeding:** Feed on demersal fish, sharks and rays as well as cephalopods and crustaceans (White et al. 2004).
Reproduction: Viviparous, 1-14 pups of 50-70cm, gestation 10-11 months. Uses shallow inshore waters as a nursery area (White & Potter 2004).	**Other information:** Listed as Vulnerable on the IUCN Red List.
Likely bioregional distribution (indicated by grey non-reef and red reef bioregions): 	

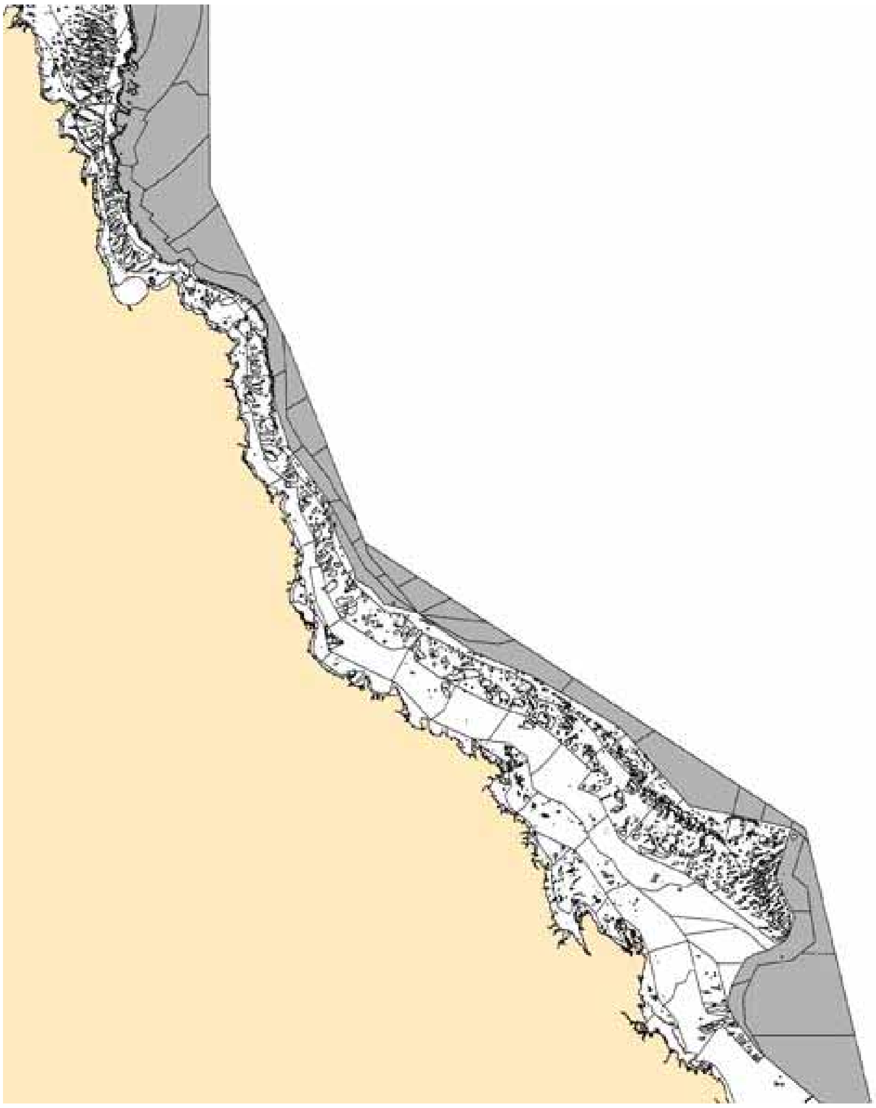
Orcinus orca (Orca)

Maximum length: 800cm	**Maximum age:** 80y
Length at maturity: Unknown	**Age at maturity:** 15y
Distribution and abundance: Extremely rare in the GBR region with an estimated density ranking of less than 1 per 100 ha.	**Feeding:** Feed mainly on large fish, but also on sharks, seabirds and other marine mammals.
Reproduction: Gestation 15-18 months, calve a single offspring every five years.	**Other information:**
Likely bioregional distribution (all offshore pelagic bioregions): 	

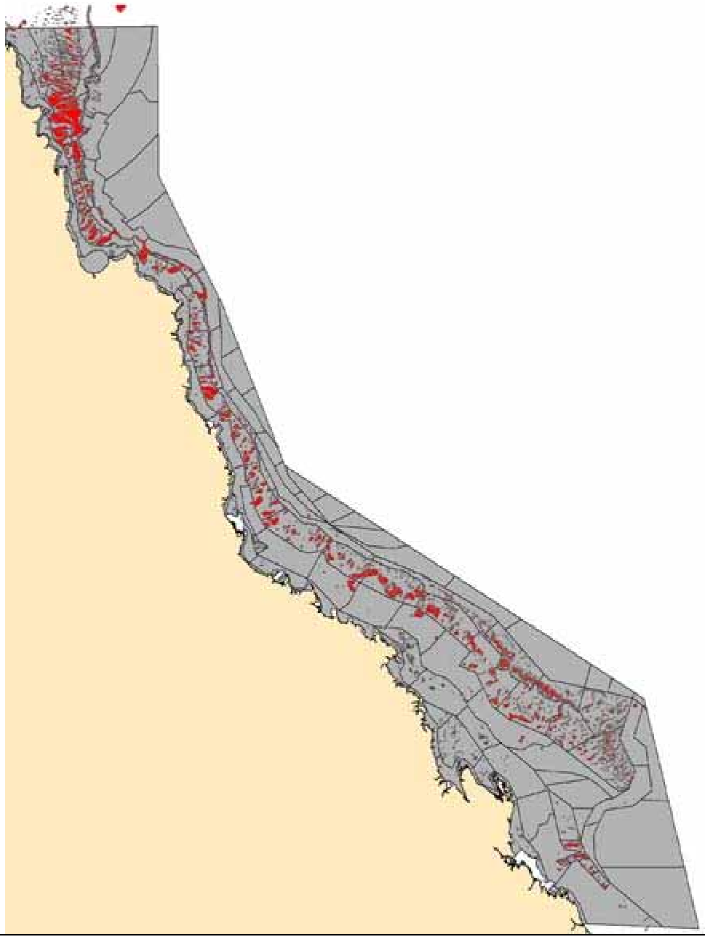
Pseudorca crassidens (False killer whale)

Maximum length: 600cm	**Maximum age:** 63y
Length at maturity: Unknown	**Age at maturity:** 10-18y
Distribution and abundance: Oceanic, prefers warmer waters. Estimated density ranking of less than 1 individual per 100 ha.	**Feeding:** Feed primarily on fish and cephalopods.
Reproduction: Females ovulate once annually, and give birth to a single calf following a 15-month gestation.	**Other information:** Has a propensity for mass strandings in Western Australia. Little is known about their migratory patterns. Pelagic cetaceans of the GBR generally not well-known (Corkeron 1994).

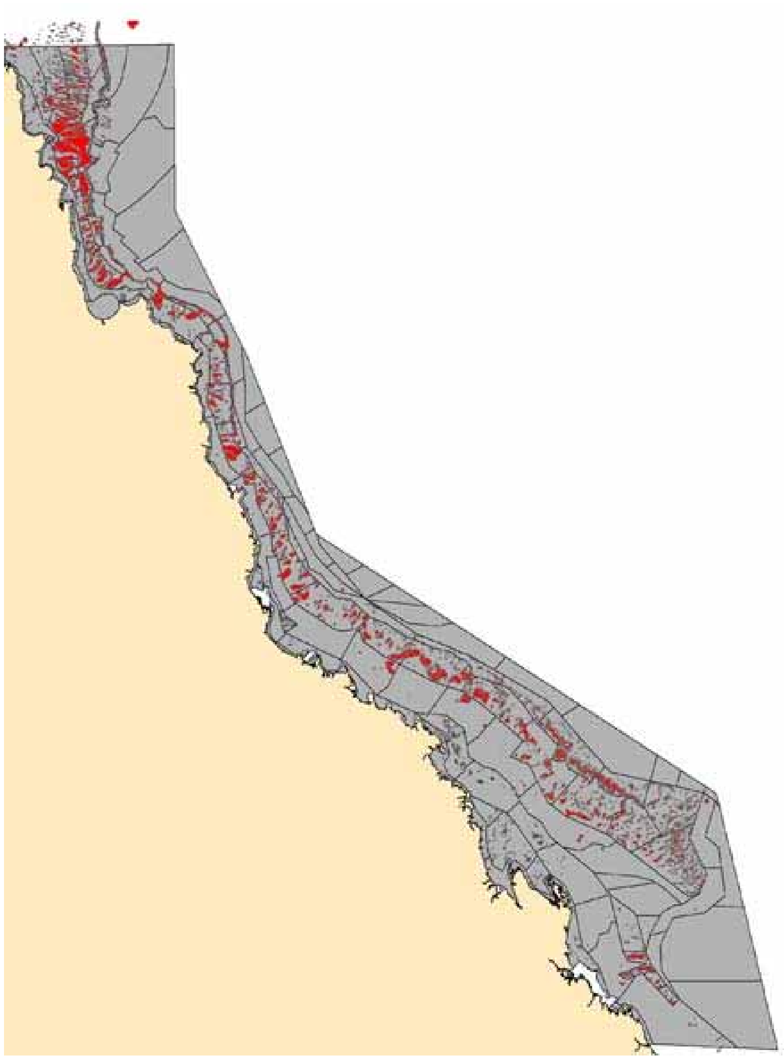
Likely bioregional distribution (all offshore pelagic bioregions):



Sphyrna leweni (Scalloped hammerhead)

Maximum length: 350cm	**Maximum age:** 35y
Length at maturity: M:140-160cm, F: 200-220cm	**Age at maturity:** M: 7-10y; F: 15y
Distribution and abundance: Coastal-pelagic and semi-oceanic. Can be seen in large schools or in shallow waters near coral reefs, occurring both inshore and offshore. Abundance: Relatively common in the GBR region, catches suggest a density ranking of around 35 individuals per 100 ha.	**Feeding:** Feeds on fish and cephalopods, sharks (Myers et al. 2007), rays and crustaceans. Also listed as predators of cetaceans (Heithaus 2001a).
Reproduction: Viviparous, 15-31 young 43-55 cm young in a litter, gestation 9-10 months	**Other information:** Often caught in GBR fisheries. Medium extinction risk is calculated for this species (Garcia et al. 2008). Regularly caught in Australian gillnet fisheries (Stevens & Lyle 1989).
Likely bioregional distribution (indicated by grey non-reef and red reef bioregions): 	

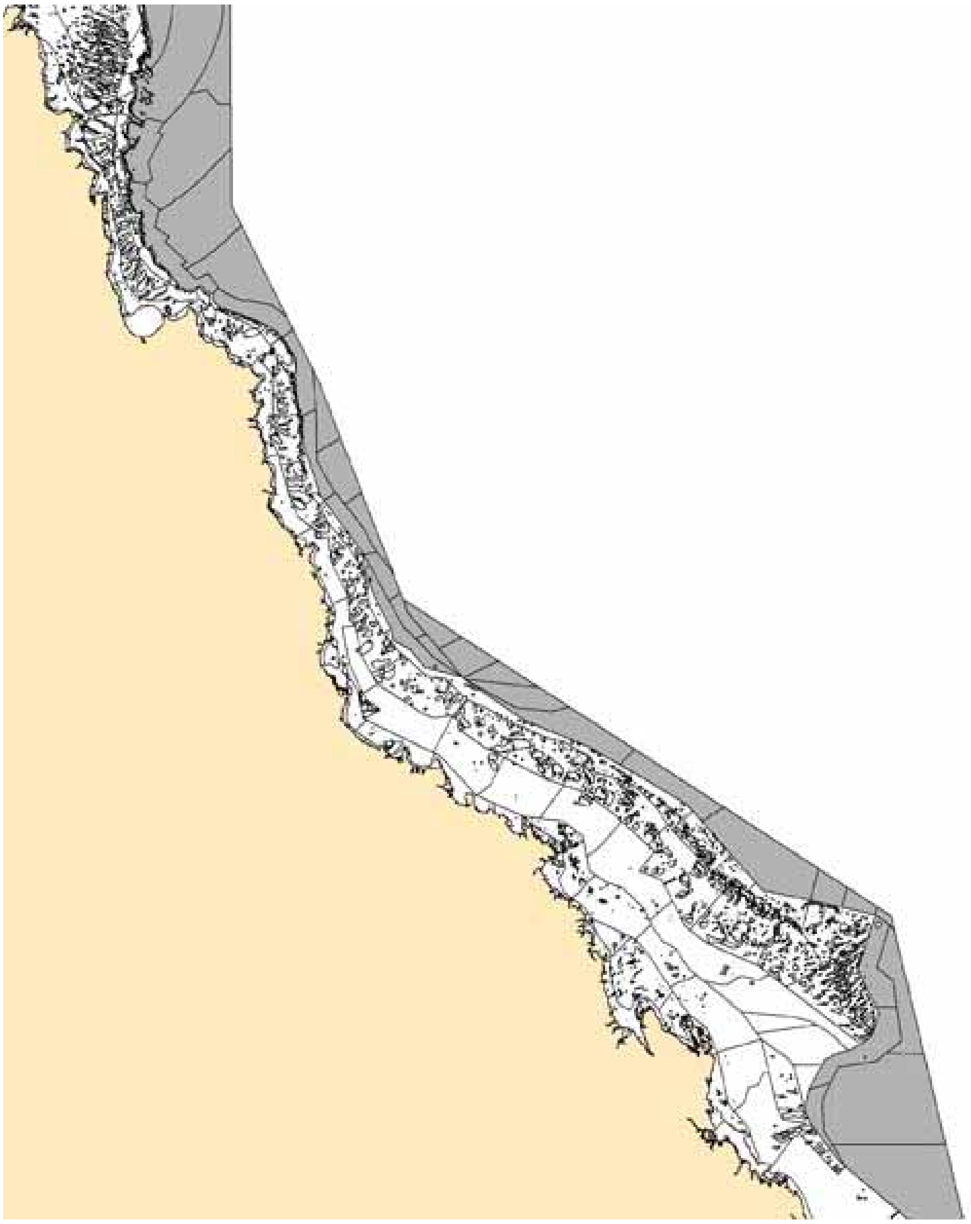
Sphyrna mokarran (Great hammerhead)

Maximum length: 600cm	**Maximum age:** 35y
Length at maturity: M:225cm, F: 210-230cm	**Age at maturity:** 15y
Distribution and abundance: Coastal-pelagic, occurring both inshore and offshore, can be seen in shallow waters near coral reefs. Abundance: Less abundant than the scalloped hammerhead, estimated density ranking of 8 per 100 ha.	**Feeding:** Feeds on fish and cephalopods, sharks (Myers et al. 2007), rays and crustaceans. Also listed as predators of cetaceans (Heithaus 2001a).
Reproduction: Viviparous, 6-33 young 50-70 cm young in a litter in Australian waters	**Other information:** Often caught in GBR fisheries (Stevens & Lyle 1989).
Likely bioregional distribution (indicated by grey non-reef and red reef bioregions): 	

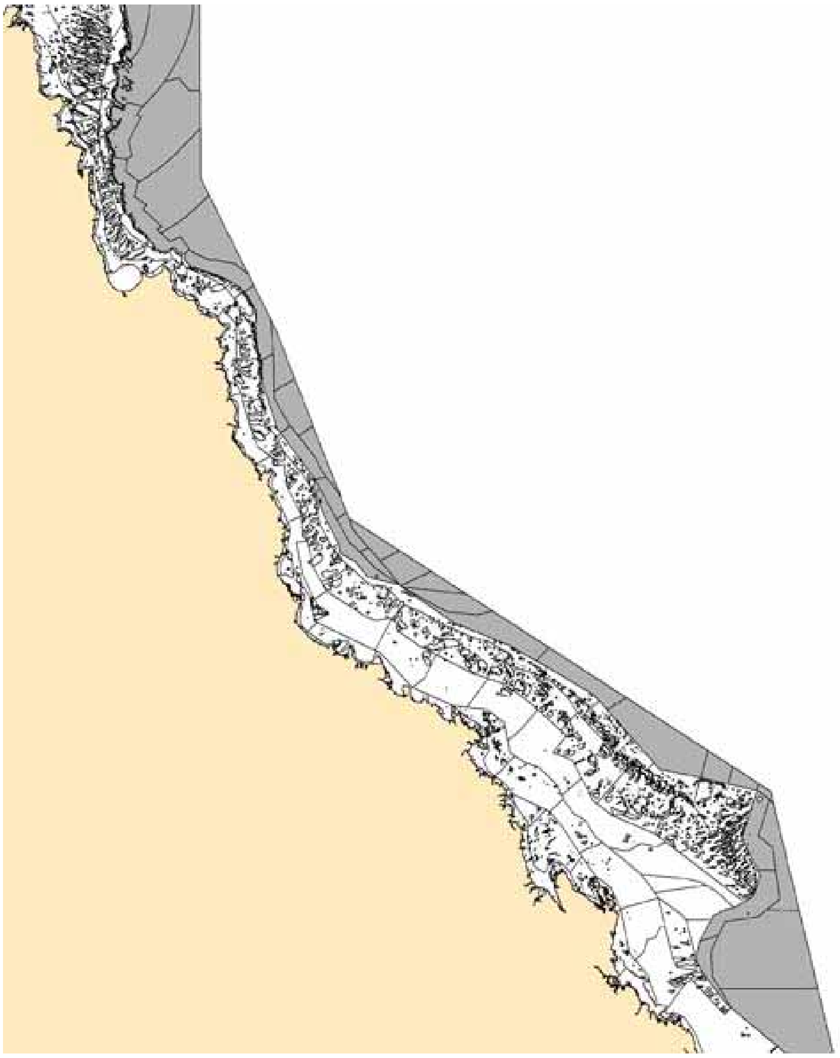
Tetrapturus audax (Striped marlin)

Maximum length: 420cm	**Maximum age:** 9y
Length at maturity: Unknown	**Age at maturity:** 2-3y
Distribution and abundance: Pelagic and oceanic, generally in cooler water than blue or black marlin. Relatively common with an estimated density ranking of 8 individuals per 100 ha.	**Feeding:** Feed on fish, cephalopods and crustaceans. Recorded as pelagic generalist top predator (Revill et al. 2009).
Reproduction: Spawning sites are between 10°S and 30°S in Southwest Pacific.	**Other information:**

Likely bioregional distribution (all offshore pelagic bioregions):



Xiphias gladius (swordfish)

Maximum length: 455cm	**Maximum age:**
Length at maturity: ~200cm	**Age at maturity:** 50% of females reach maturity at ~10y
Distribution and abundance: Oceanic and pelagic. Catches suggest an estimated density ranking of 40 individuals per 100 ha.	**Feeding:** Feed on fish and cephalopods.
Reproduction: Spawning between September and May, in warm EAC waters of the Coral Sea (Young & Drake 2002). fecundity: 1.2-2.5 million eggs	**Other information:** One of four pelagic species targeted by Australian longline fishery. 90% of females caught at less than 10 years old, concern that they are immature. Recorded shift in catch data from older to younger swordfish 1997-2001. Other fisheries with large catches of immature females have shown steep declines (Young & Drake 2002).
Likely bioregional distribution (all offshore pelagic bioregions): 	

Distribution of species among habitats

Coral reefs

Apex predators that spend time on coral reefs include tiger sharks and bull sharks, the two hammerhead sharks, pigeye sharks, silvertip sharks and lemon sharks. Tiger sharks range throughout all GBR habitats, while the bull and pigeye sharks are found in all habitats except the oceanic and deep water habitats. Lemon sharks can exhibit some degree of natal site fidelity, but migrate throughout coastal areas of the GBR and may range over considerable distances (Schultz et al. 2008). These seven species are likely to prey on the reef's generalist top predators. For instance, grey reef sharks have been recorded in the stomachs of silvertip sharks (Randall 1977).

Coral reef predator communities are characterised by resident generalist top predators dominated by serranids (cods, trouts and groupers), red bass and the blacktip, whitetip and grey reef sharks. The coral trout species *Plectropomus leopardus* and *P. laevis* are estimated to make up 33% of the GBR grouper fauna, and their presence on reef crests and reef fronts is considered a unique feature of the GBR predator fauna (Choat & Russell 2008). These resident predators are site-attached at a range of spatial scales, from relatively small territories within a reef (Zeller & Russ 1998; Papastamatiou et al. 2009), to home ranges encompassing a whole reef. This group of predators is likely to play the most easily defined role of regulating prey recruitment, abundance, species composition, diversity and behaviour (Hixon 1991). Transient generalist top predator populations on coral reefs include primarily larger sharks and barracudas.

The AIMS Long Term Monitoring Program includes regular counts of the most abundant coral reef predators; primarily those in the generalist top predator category. There is both cross-shelf and latitudinal variability in their density.Common coral trout *P. leopardus*, the most abundant of the generalist top predators, predominates on the mid shelf reefs of the southern GBR (

Figure **2**). The red bass *Lutjanus bohar* and the bluespot coral trout *P. laevis* are most abundant on the outer shelf reefs of the northern GBR. The bar-cheeked coral trout *P. maculatus* is characteristic of inner shelf reefs of the central GBR. Even within reef habitats there can be variability in the density, and therefore presumably the intensity of the influence, of generalist top predators. For instance, *P. leopardus* densities tend to be highest on reef slopes and seaward edges of lagoons, where they can be as high as 32 individuals per 1,000m^2 on the southern GBR (Kingsford 2009).

Interestingly, the AIMS Long Term Monitoring Program data revealed a significant positive correlation between densities of prey (damselfish densities expressed as individuals per 100m^2) and resident coral reef predators when the very high predator densities in one GBR sector were treated as an outlier and removed (Figure 3). This suggests that higher densities of resident predators do not necessarily lead to depleted prey populations. Emerging comparisons between fished and unfished deeper inter-reefal habitats of the GBR are revealing that unfished areas host greater numbers of both predator and prey species (Cappo et al. 2009).

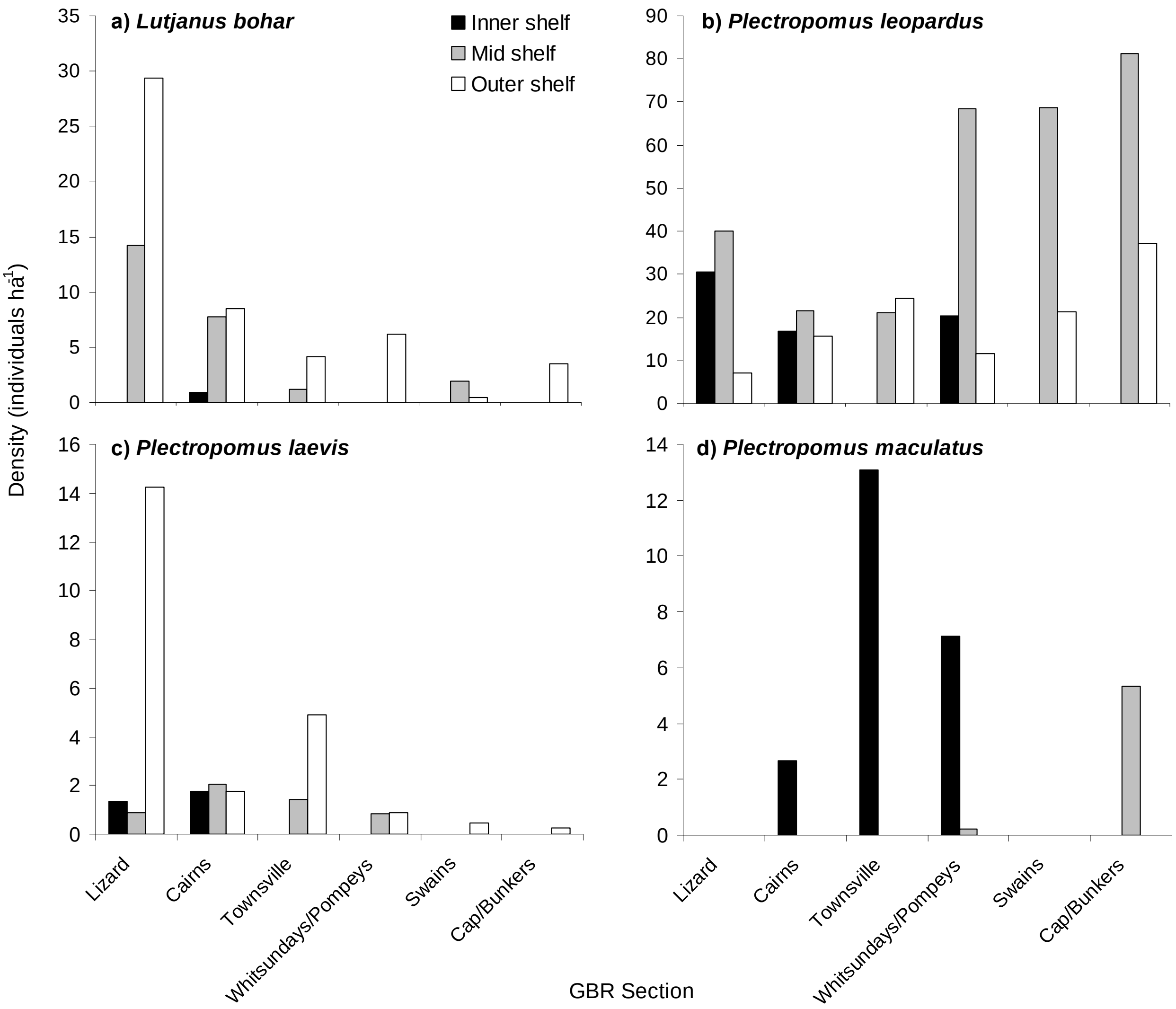


Figure 2. Mean density (individuals per hectare) of common species of coral reef top predators recorded by the AIMS Long Term Monitoring Program. Species distributions are shown by inner, mid and outer shelf reefs of each Great Barrier Reef section. Note differences in y-axes.

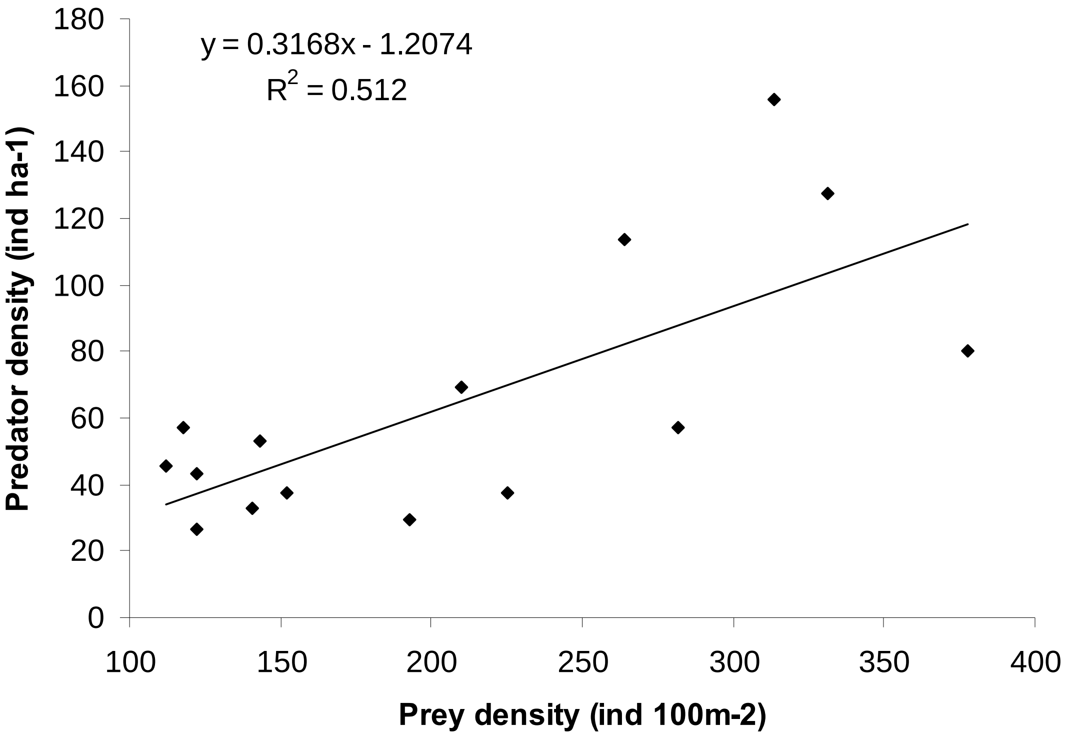


Figure 3. Relationship between prey and predator densities on the GBR. Data from AIMS Long Term Monitoring Program counts, expressed as a linear term.

Individual species profiles – Important coral reef predators

Plectropomus laevis (bluespot coral trout)

Maximum length: 120cm	**Maximum age:** 15-18y
Length at maturity: 35-45cm	**Age at maturity:** 2-4y
Reproduction: Protogynous hermaphrodite; sex change between 45-85 cm TL. Spawning after new moon between Sept and Dec. Forms spawning aggregations of up to 100 individuals.	**Feeding**: Piscivorous generalists
Distribution: *Plectropomus laevis* is most abundant on the front of outer shelf reefs (Figure **2**) and is more abundant on the northern GBR with a steady decrease in abundance toward the southern end of the reef (Figure 4). Larger bluespot colour form individuals appear to actively move toward outer shelf reefs.	

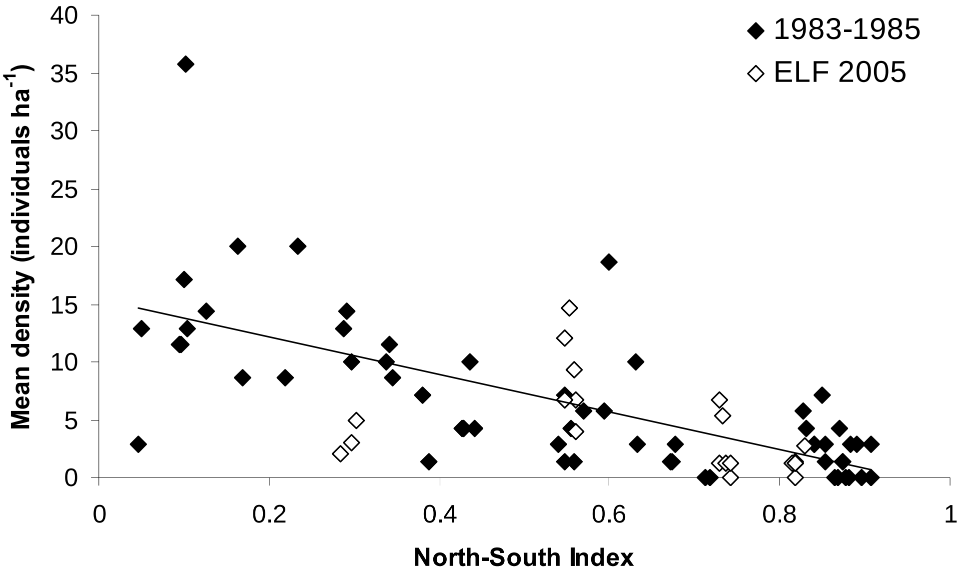


Figure 4. Latitudinal trends in *Plectropomus laevis* density on outer shelf reefs. North-South Index of 0 = Tip of Cape York (N); 1 = Lady Elliot Island (S). Data from 1983-85 (with regression line) and from the ELF (Effects of Line Fishing) Experiment 2005 are shown.

Abundance: Maximum abundance on far-northern outer shelf reefs ranges from 20-35 per ha; on southern outer shelf reefs abundance ranges from 0-7 per ha. On all mid shelf reefs densities are usually less than 5 per ha.

Fishing: Minimum retainable size 50 cm TL, Maximum retainable size 80 cm TL. Total Allowable Commercial Catch (all coral trout combined) = 1350 tonnes.

Plectropomus leopardus (common coral trout)

Maximum length: 70cm on most of GBR; 90-100 in Capricorn-Bunker group.	**Maximum age:** 15-16y; only 5% of population >10y old.
Length at maturity: 25-35cm	**Age at maturity:** 1-3y
Reproduction: Protogynous hermaphrodite; sex change between 25-62 cm TL (most 30-50 cm). Spawning after new moon between Sept and Dec. Forms spawning aggregations of up to 300 individuals.	**Feeding**: Piscivorous on a wide variety of reef fish, including pomacentrids, hardyhead bait fish, small parrotfishes and fusiliers. This species often aggregates to feed.

Distribution: *Plectropomus leopardus* is most abundant on outer mid shelf reefs and is on average more than twice as abundant on the southern half of the GBR than on the northern half (Figure 5).

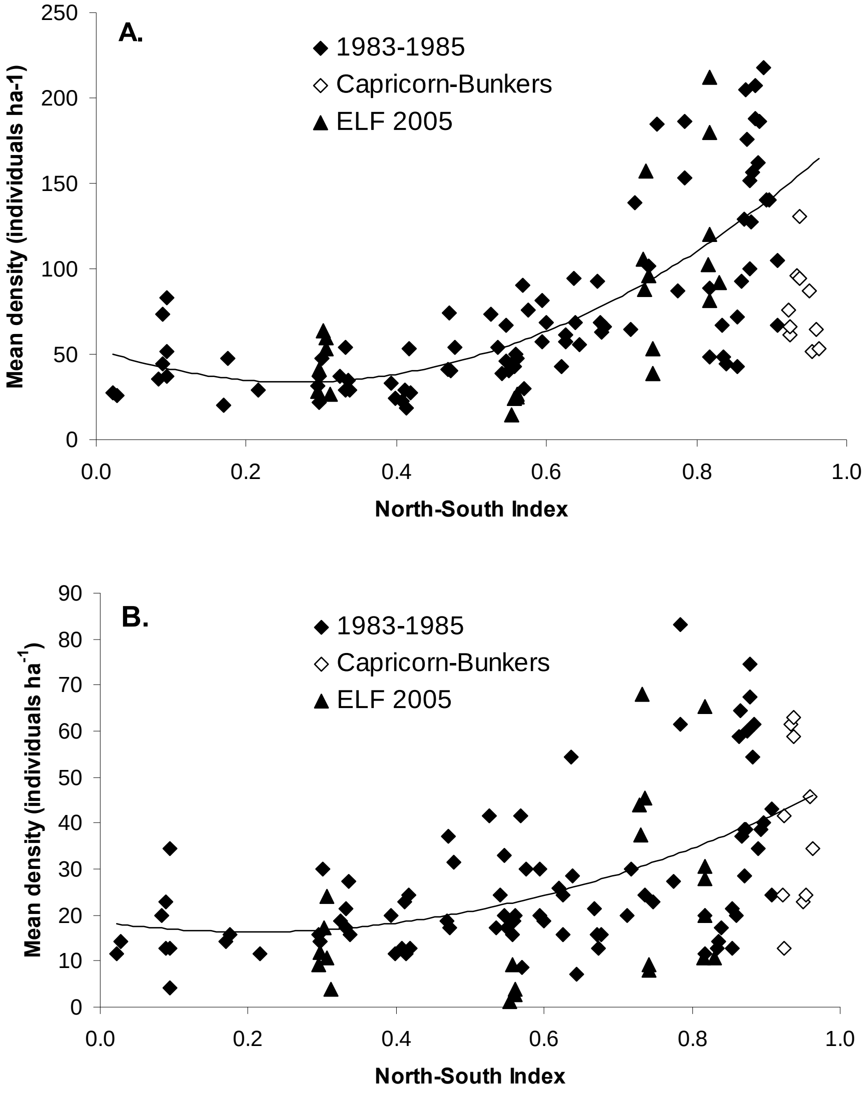


Figure 5. Latitudinal trends in total (A) and adult (B) *Plectropomus leopardus* density on mid shelf reefs. North-South Index of 0 = Tip of Cape York (N); 1 = Lady Elliot Island (S). Data from all reefs 1983-85 (regression lines), from the Capricorn Bunker group only, and from the ELF (Effects of Line Fishing) Experiment 2005 are shown.

Abundance: Overall abundance on northern mid shelf reefs ranges from 20-35 per ha; on southern outer shelf reefs abundance ranges from 0-7 per ha. On all mid shelf reefs densities are usually less than 5 per ha (Figure 5).

Fishing: Minimum retainable size 38 cm TL, Total Allowable Commercial Catch (all coral trout combined) = 1350 tonnes.

Plectropomus maculatus (barcheek coral trout)

Maximum length: 75cm	**Maximum age:** 15-16y
Length at maturity: 25-35cm	**Age at maturity:** 1-3y
Reproduction: Protogynous hermaphrodite; sex change usually between 30-50 cm. Spawning after new moon between Sept and Dec. May form spawning aggregations.	**Feeding**: Piscivorous on a wide variety of reef fish.

Distribution: *Plectropomus maculatus* is only abundant on inner shelf reefs (

Figure **2**) and is most abundant on very turbid coastal and island fringing reefs. There was no apparent latitudinal pattern in the distribution of this species (Figure 6).

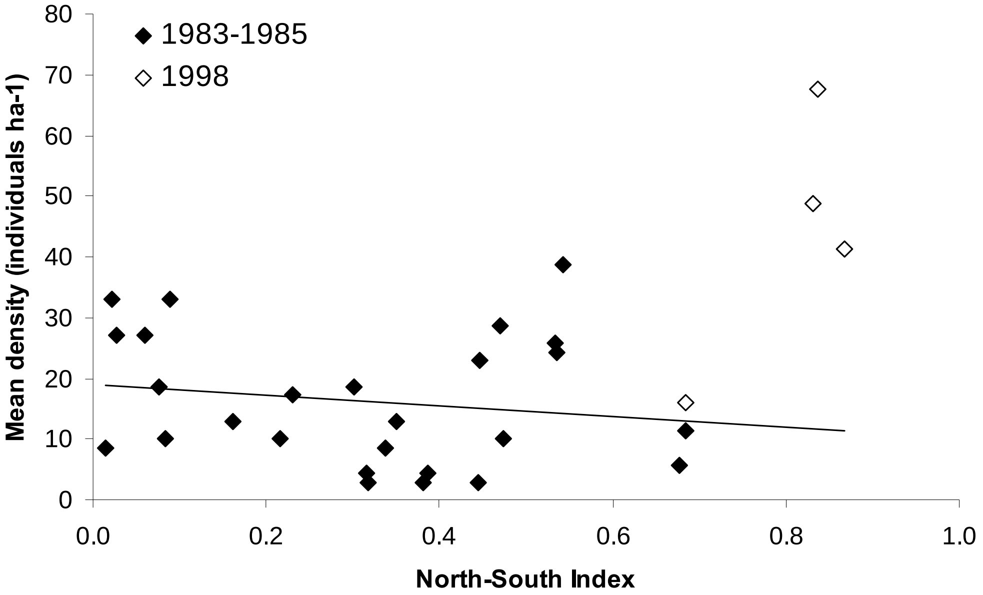


Figure 6. Latitudinal trends in total *Plectropomus maculatus* density on inner shelf reefs. North-South Index of 0 = Tip of Cape York (N); 1 = Lady Elliot Island (S). GBR wide data from 1983-85 (regression line) and from the Whitsundays and Shoalwater Bay in 1998 are shown.

Abundance: Overall abundance of *P. maculatus* ranged from 5-40 per ha in 1983-85. Recent densities measured on protected inshore reefs have ranged from 40-80 per ha

Fishing: Minimum retainable size 38 cm TL. Primarily targeted by the recreational fishery. Totoal Allowable Commercial Catch (all coral trout combined) = 1350 tonnes.

Lutjanus bohar (red bass)

Maximum length: 90cm	**Maximum age:** 50-60y; 85% of shallow water population are less than 10 years old
Length at maturity: M: 30cm (functionally mature at 45-50 cm); F: 43 cm	**Age at maturity:** M: 1-2y; F: 9y
Reproduction: Separate sexes. Spawning between August-April; peak spawning probably November.	**Feeding**: Piscivorous on a wide variety of reef fish. Mainly nocturnal feeders.
	Abundance: Recent abundance estimates of *Lutjanus bohar* ranged from 5-30 per ha in the Lizard Island area and from 1-10 per ha in the Townsville area. South of Cape Upstart this species was only seen occasionally on clear outer shelf reefs. **Fishing**: No–take (protected) species. This species is reputed to be ciguartoxic and cannot be retained by fishermen.

Distribution: *Lutjanus bohar* is most abundant on outer shelf reefs (

Figure **2**). Larger fish are apparently more abundant in deeper water (30-50 m depth) where 75% of individuals were over 10 years old, compared to only 15% is shallow reef waters. On mid shelf reefs *Lutjanus bohar* were most abundant in the Far North and Lizard Island area and were rare south of Cape Upstart (Figure 7). On outer shelf reefs this species was also most abundant in the north with low numbers in the Pompeys, Swain and Capricorn-Bunker reefs. This species often forms large resting schools during the day.

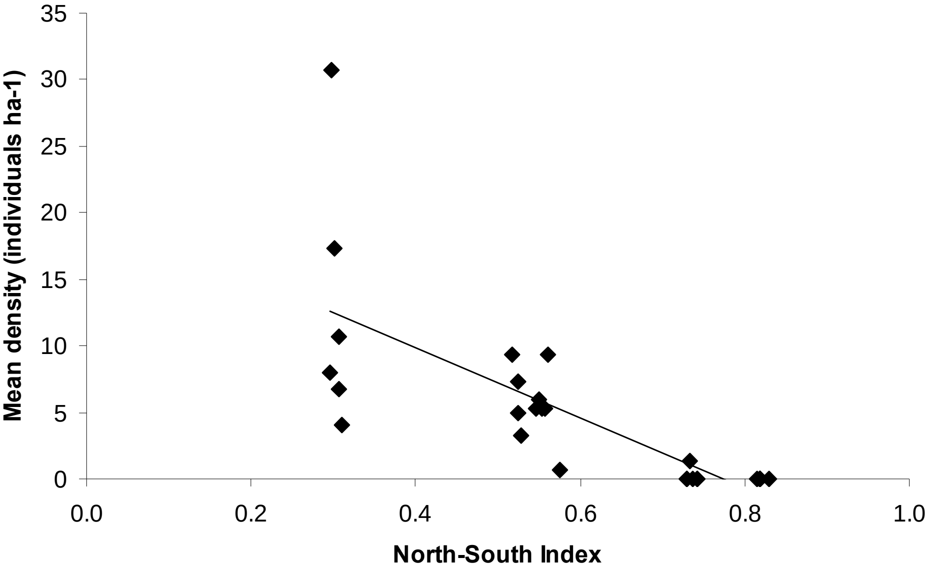


Figure 7. Latitudinal patterns in the abundance of *Lutjanus bohar* on mid and outer shelf reefs. North-South Index of 0 = Tip of Cape York (N); 1 = Lady Elliot Island (S). Data from the ELF (Effects of Line Fishing) Experiment.

Inshore and inter-reef habitats

Very little information exists on the extensive inshore and inter-reef shoals and soft-bottom habitats of the GBR. The benthic communities in these areas have been examined to some extent, and include sponges, gorgonians, alcyonarians, corals and marine plants, but less research has been done on fish communities that use these habitats. Generally, fish are more diverse and abundant in areas that are more structurally complex, such as shoals or aggregations of benthic organisms on emergent hard substrata, than on featureless soft sediment areas (Speare et al. 2008). The differences in both the benthic communities and the assemblages of mobile organisms that use them are most probably shaped by cross-shelf variation in sedimentary processes and along-shelf variability in oceanic influences, including combinations of storms, tides, currents, upwellings, waves, riverine flows and seasonal wind patterns. These environmental characteristics shape the physical environment (e.g. topography, sediment grain size and composition, water chemistry) and therefore influence the availability of benthic communities for the recruitment, feeding and habitat of larger and more mobile species. Clear latitudinal boundaries in fish community structure, which correlate with substratum composition gradients and specific current and tide interactions, exist at Bowen, Townsville and Cape Flattery (Cappo et al. 2007).

The fish assemblages that use these habitats are further influenced by biogeography, oceanographic processes and ontogenetic changes in habitat use (Speare & Stowar 2008). Apex predators likely to be important in inshore habitats are the bull shark *Carcharhinus leucas*, the scalloped hammerhead *Sphyrna leweni* and the estuarine crocodile *Crocodylus porosus*. Crocodile densities are assessed along the Queensland coast regularly, but surveys are generally restricted to waterways outside the boundaries of the GBRMP (QPWS 2007), and it is difficult to estimate how many crocodiles would use GBRMP waters to feed or travel. Satellite tracking suggests that estuarine crocodiles are temporary migrants within the GBRMP (GBRMPA 2005), and may only play a minor role as a predator. Bull sharks *Carcharhinus leucas* are likely to be more influential as an inshore predator than crocodiles. The tiger shark *Galeocerdo cuvier* has been found to be important in non-reef habitats of the outer half of the shelf (Cappo et al. 2007), but also dominates catch data from the Queensland Shark Control Program, which comes from coastal nets and drumlines. The silvertip *Carcharhinus albimarginatus* is a relatively abundant member of the deeper offshore non-reef environments (Cappo et al. 2007). The extent to which the grey nurse shark plays a role on the GBR is not well understood, but it is likely to be restricted to inshore areas of the southern GBR (Environment Australia 2002).

Generalist top predators that are likely to be most important in these habitats include a variety of non-reef and inshore shark species (Figure 8), large cods and groupers and transient mackerels and barracudas. The makeup of the substratum is likely to play an important role on species composition; for instance, the coral trout *P. maculatus* is correlated with hard bottom habitats, while the mackerel *Scomberomorus queenslandicus* and trevallies are more commonly found over soft-bottom areas (Speare et al. 2008). The abundance of the lemon shark *Negaprion acutidens* is correlated with shallow outer shelf areas (Cappo et al. 2007). Some species, such as the Spanish mackerel *S. commerson*, undertake regular or seasonal migrations associated with reproductive seasons (Ballagh et al. 2006) and they may exert seasonal pulses of stronger predation pressure on communities along migratory pathways.

Many species that use coral reefs or offshore habitats as adults use shallow coastal embayments as nursery areas, including some of the most common non-reef sharks of the GBR (White & Potter 2004) and some of the large groupers. Large groupers of the genus *Epinephelus* are relatively rare, with densities of less than one individual per 1,000 m^2 being typical even in preferred habitats (Pears et al. 2006). Evidence suggests that as for coral reef species, generalist top predators that use inshore and inter-reef habitats also exhibit habitat partitioning, both across the shelf and latitudinally (Cappo et al. 2007).

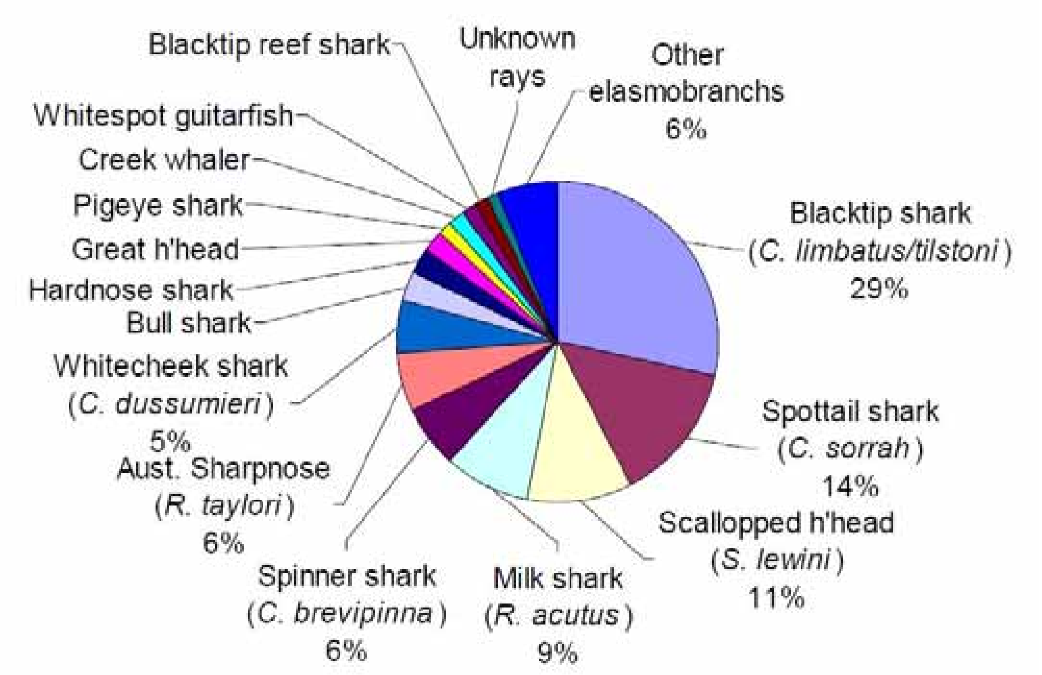


Figure 8. Proportions of inshore shark species caught in the East Coast Inshore Finfish Fishery (n = 2,345). Figure supplied by Dr. Colin Simpfendorfer, Fishing & Fisheries Research Centre, JCU.

While most GBR cetaceans considered here occur in offshore pelagic waters, two generalist top predators (Australian snubfin dolphin *Orcaella heinsohni* and Indo-Pacific humpbacked dolphin *Sousa chinensis*) are inshore specialists and occur in most of the major GBRMP embayments. Both species are frequently associated with turbid, highly productive nearshore environments (Parra et al. 2006).

Pelagic and deep water habitats

While some research has established the trophic structure of offshore pelagic species that occur in GBRMP waters beyond the reef itself, virtually nothing is known about the role and importance of deep-water predators of the continental shelf. Many deepwater sharks are likely to play an important role in demersal and benthic communities of the outer continental shelf and upper continental slope, along with a number of tuna, mackerel and billfish species that occupy the generalist top predator role in the offshore pelagic ecosystem. Much of the information about the distribution and abundance of these species comes from longline fisheries that operate beyond the GBRMP boundaries.

The pelagic system supports the largest variety of apex predators, including orcas and great white sharks, which can be considered the highest-level apex predators on the GBR although their importance is diminished by their relative rarity on the GBR. More common pelagic apex predators include large pelagic sharks such as the shortfin mako, the silky shark and the oceanic whitetip. These are likely to play a more consistent predatory role at the top of pelagic food webs (Revill et al. 2009). Large billfish, such as the swordfish and striped marlin, are also important pelagic predators and are probably abundant on a seasonal basis, as they gather inside the GBRMP to spawn (Pepperell & Davis 1999; Young & Drake 2002). Most of these species are also found on rare occasions around outer shelf and outer midshelf reefs.

Trophic pathways and the role of different functional groups in deep water environments are poorly understood. Species of predators occupying the deeper waters of the continental slope are understood to be relatively rare and sedentary (Chin & Kyne 2007), and continental slope sharks such as the sevengill shark *Heptranchias perlo* are likely to occupy the top predatory role in this habitat (Braccini 2008). Many of the predatory dolphins are known to feed primarily on squid, and are therefore likely to have a lesser impact as top predators, despite their generally high MTI rating (Pauly et al. 1998b). However, some are voracious predators of pelagic fish, and can compete with tiger sharks for prey (Heithaus 2001a).

THE ROLE OF APEX PREDATORS ON THE GBR

Research and knowledge of sharks and other predators has been sporadic and patchy on the GBR (Chin & Kyne 2007). As elsewhere, a long history of fishing means that it is difficult to determine whether current populations of predators are still performing their functional roles, and no data exists from before fishing began (Jackson 2001). The research that has been done has often been driven by the need for fisheries management information, as most of the predators on the GBR are important to fisheries. The role of each predator species, as well as that of the functional group as a whole, is not uniform across the GBR, much like the role and importance of herbivores varies across the continental shelf (Hoey & Bellwood 2008). As seen above, it is also likely that the relative importance of the role played by apex predators, generalist top predators and high-level mesopredators varies according to their relative abundance and the complexity of the ecosystem.

On **coral reefs**, the most complex of GBR ecosystems, abundant resident generalist top predators are possibly more important than larger, rarer and more transient apex predators (Gaston & Fuller 2008). Large snapper, trout and emperors are abundant and even though their densities vary cross-shelf and latitudinally (Williams & Russ 1994) all reefs that have not been heavily fished support a number of generalist top predators. These are likely to locally affect the density and behaviour of mesopredators (such as smaller cods and groupers), which in turn will play a role in regulating recruitment, abundance and behaviour of smaller fish at lower trophic levels (eg. Stallings 2008).

However, it is likely that reef sharks play a differing role depending on their densities. They are probably more important on reefs protected from fishing than those where their densities have been greatly reduced (Robbins et al. 2006). It is possible that where they have been intensively fished, larger reef sharks are functionally obsolete. This is difficult to ascertain because studies on protected reefs tend to focus on target species, rather than the other components of the ecosystem; and the complexity of coral reefs makes it very difficult to assess the role of predation in shaping the ecosystem.

Inshore and inter-reef habitats are generally less complex than coral reefs, apart from sometimes ephemeral islands of complexity such as seagrass beds, shoals and *Halimeda* banks (Speare & Stowar 2007; Speare et al. 2008). Many predators use inshore areas as nursery grounds, and inter-reef soft bottom habitats harbour populations of large, transient, wide-ranging predators (Stowar et al. 2008), including some of the larger non-reef sharks. Estuarine apex predators such as estuarine crocodiles may prey on large organisms during part of their life cycle when they rely on inshore marine areas or even land (e.g. nesting marine turtles in northern Australia) (Heithaus et al. 2008b). Some species are likely to use inshore, inter-reef and reef habitats during their life cycle, effectively creating large-scale trophic connectivity pathways. Predation may be more important here than on coral reefs in shaping community structure, even though their local densties may be lower. Changes in behaviour of prey in response to the risk of predation can be significant even when actual predation events are infrequent (Heithaus et al. 2008a).

Research on remote inshore habitats has identified at least four trophic levels in the GBRMP (Abrantes & Sheaves 2009). However, studies comparing open and closed areas in these habitats are rare, and the transient nature of many species that use inshore areas makes it difficult to separate the effects of protection from background variability (Speare et al. 2008). Even studies that found clear increases in the numbers of targeted predators on unfished shoals of the southern GBR (Cappo et al. 2009) did not conclusively demonstrate differences in other elements of the ecosystem, such as prey species or benthic communities (Stowar et al. 2008). A comparison of estuaries open and closed to fishing adjacent to the GBRMP revealed similar results – significantly higher predator abundance in areas closed to fishing, but no differences in the structure of prey communities (Ley et al. 2002). The transient nature of larger apex predators that utilise these habitats may override the effects of the more sedentary, local generalist top predators. It may also be that the high turnover rates in some of these systems provide an inherent resilience to changes in predation levels (Ley et al. 2002).

Pelagic and deep water habitats are perhaps the simpest GBR ecosystems, due in part to the relatively oligotrophic nature of Australia's offshore waters. There are no permanent upwelling features, although seasonal aggregations of organisms form in pelagic outer shelf and offshore areas. For instance, black marlin aggregate seasonally outside the outer barrier off Cairns where their spawning aggregation is targeted heavily by the charter fishing industry (Speare 2003; Brewer et al. 2007). There is literature that suggests that deep-water sharks are the most vulnerable to overfishing, and that predators are very important in shaping these relatively simple systems (reviewed by Baum & Worm 2009).

Ecological Role

Prey abundance

Large apex predators, especially sharks, are often attributed the role of regulating populations of prey species (Myers et al. 2007). Population modelling and research suggests that tiger sharks *Galeocerdo cuvier* control population size and behaviour of seabirds (Stevens et al. 2000), marine turtles (Heithaus et al. 2007a) and dugongs (Wirsing et al. 2007a) in Shark Bay, Western Australia. However, it is difficult to assess the effects of apex predators on GBR prey populations or ecosystems, as the impacts of predators are confounded by differences in habitat complexity, larval dispersal and population dynamics of prey (DEH 2005). Most studies investigating the effects of predator removal indicate a prey-release response, where prey species increase in abundance following the removal of predators, causing flow-on effects on their food resources. Prey release has been documented for a number of ecosystems (Hughes 1994; Steneck 1998; McClanahan et al. 1999; Myers & Worm 2003). The complexity of coral reef ecosystems, the diversity of fish and other prey species and the opportunistic nature of many predators make it difficult to establish trophic relationships (Graham et al. 2003).The role and importance of predators on the GBR is perhaps best evaluated when comparing areas where they have been removed with those that have historically been protected from fishing.

Blue (open to fishing), Green (no-take) and Pink (no-go) Zones of the GBR are traditionally compared to observe the effects of protection from fishing. Studies of this type exist primarily for coral reef habitats of the GBR (Evans & Russ 2004), but have more recently also been conducted in estuarine habitats (Ley et al. 2002) and on inter-reefal shoals (Speare et al. 2008; Stowar et al. 2008). Many of these studies report only on the effects of protection on the predators themselves, as they are the primary fisheries target species. Those that extend their research into prey communities have found equivocal results. While most report little or no change in composition or abundance of prey communities, some have found a correlation between increased predator abundances and declines in common prey species. For instance, after 14 years of protection from fishing, Green Zones in the Whitsunday and Palm Island groups had biomass of *P. leopardus* 3-4 times higher than fished zones, and prey species preferred by *P. leopardus* were significantly reduced in density (Graham et al. 2003). This indicates a top-down role for this species in controlling population sizes of prey species. However, some prey species did not decline, including the wrasse *Halichoeres melanurus* and the parrotfish *Chlorurus sordidus* (Graham et al. 2003). Other studies found no flow-on effects of protecting predators on two species of non-target fishes (Evans & Russ 2004) or on species composition and diversity of prey (Ley et al. 2002). For the most part, the role of predators in controlling prey abundance on the GBR remains unknown.

Fish recruitment

Competition and predation are the two primary biological factors affecting density-dependent mortality during reef fish recruitment on the GBR. A number of GBR-based studies have attributed the primary effect to either one or the other, but most researchers agree that they probably operate synergistically (Figueira et al. 2008). Competition appears to be more important where prey abundance is low compared with the availability of refuges (Hixon & Jones 2005), indicating a lesser role of predation in areas of high habitat complexity. This suggests that predators may be more important in affecting prey recruitment in relatively uniform soft-bottom, inshore and pelagic environments when compared with coral reefs.

Generalist top predators on the GBR have been shown to significantly reduce coral reef fish recruitment. A small-scale experimental study conducted at Lizard Island found that resident high-level piscivores reduced settlement of butterflyfish, surgeonfish, rabbitfish, and most damselfish, and the highest levels of predation pressure prevented recruitment of butterflyfish and rabbitfish altogether (Almany 2004). A meta-analysis of six studies on early post-settlement mortality of 24 species of reef fishes – 10 of which were carried out on the GBR – found that an estimated 55.7% (CI: 43.0–65.5%) of juveniles were consumed within 1–2 days of settlement (Almany & Webster 2006). Furthermore, the results of this study strongly suggested that prey mortality rates were species-specific. Such high species-specific predation pressure is likely to have a strong influence on the development of reef fish community structure. Similar studies are not available from inshore, inter-reef and pelagic communities on the GBR.

Diversity, community composition and trophic structure

Predation pressure can affect the species composition of prey communities, depending on the nature and magnitude of predator selectivity (DeMartini et al. 2008). At smaller scales, GBR research has shown that the magnitude of a predator's role depends on whether they are selective in their consumption of prey, and if they are selective, whether they choose dominant or inferior competitors, or abundant or rare species. Furthermore, predation on coral reefs can alter reef fish diversity, especially when rare prey species may be at greater risk from predation than common ones (Almany & Webster 2004). Predators may affect rare prey both directly through consumption and indirectly by affecting the diversity of trophic levels lower than immediate prey species (Graham et al. 2003). Predation can also change competitive interactions between prey, whereby the outcomes of competition for food, space and other resources can be altered by different predation pressure on one competitor (Hixon & Jones 2005). As seen in both estuaries and on coral reefs, however, highly diverse and productive communities at lower trophic levels may mask the effects of variations in predator densities (Ley et al. 2002).

A recent small-scale study in the Bahamas showed that the increased abundance of a top predator (Nassau grouper *Epinephelus striatus*) reduced the feeding activity of medium-level predators (coney grouper *Cephalopholis fulva* and graysby grouper *C. cruentata*), thereby indirectly increasing the recruitment of smaller prey species (Stallings 2008). The depletion of apex predators has been found to release mesopredators from predation pressure, causing their numbers to increase and exerting pressure on lower trophic levels (Myers et al. 2007).

Studies in the Pacific have documented a number of differences in herbivore and benthic communities in response to a gradient in predator densities, suggesting a strong link between predatory and herbivorous functional groups. However, this pattern was confounded by the fact that in Hawaii, large parrotfishes are also targeted by artisanal fisheries (Friedlander & DeMartini 2002). Unfished reefs with high predator abundances were characterised by drummers (Kyphisodae), spectacled parrotfish (*Chlorurus perspicillatus*), whitebar surgeonfish (*Acanthurus leucopareius*) and greenfin parrotfish (*Chlorurus sordidus*). The authors of these studies state that “The reefs in the north-western Hawaiian islands (NWHI) are among the few remaining large-scale, intact, predator-dominated reef ecosystems left in the world and offer an opportunity to understand how unaltered ecosystems are structured, how they function, and how they can most effectively be preserved.” (Friedlander & DeMartini 2002). Their ‘inverted trophic pyramid’, with apex predators making up the largest proportion of the fish biomass (Sandin et al. 2008), is at odds with the more traditional relationship between body size and density, where smaller species are found in greater numbers – and biomass – than larger ones (Ackerman & Bellwood 2003). But are all reefs in their natural state dominated by predators? Are the predator densities and biomass recorded on isolated oceanic reefs in the central Pacific representative of large, contiguous continental shelf reefs, such as the GBR? On the GBR, the only equivalent information could come from Green and Pink Zones that have been effectively closed to human access for at least 20 years.

Few studies consider the effects of marine protected areas (MPAs) on non-targeted species, and those that do have found differing results. MPAs in the Houtman Abrolhos Islands in Western Australia have resulted in differences in species assemblage structure. Non-target fish species were either more abundant in fished zones (wrasses *Coris auricularis, Thalassoma lutescens, Thalassoma lunare,* and damselfish *Dascyllus trimaculatus*), or unfished zones (morays *Gymnothorax spp,* drummer *Kyphosus sydneyanus,* parrotfish *Scarus microhinos,* damselfish *Chromis westaustralis,* and butterflyfish *Chaetodon spp.*), with a greater diversity of herbivorous fish in the unfished zone (Nardi et al. 2004). This pattern was supported by a study along a fishing gradient on Fijian reefs, where all functional groups of fish, except territorial omnivores, had greater biomass in areas of lower fishing intensity (Dulvy et al. 2002). Other studies, including on GBR reefs, show no effect of MPAs on non-target species and benthic communities (Williamson et al. 2004; Ayling & Choat 2008). Studies in the Pacific have shown that gradients in exploitation pressure can affect the amount and type of herbivory occurring, with more large roving grazers on unfished or lightly fished reefs and greater numbers of turf-farming damselfish on more heavily fished reefs (Dulvy et al. 2002; Sandin et al. 2008). There was a marked association between high predator abundance and high coral cover, and it appeared that unfished reefs had a greater capacity to recover from disturbances. Ayling and Choat (2008) also found a positive association between high predator abundance and coral cover on the central Great Barrier Reef, but more detailed investigations are required to confirm this as a clear correlation.

Behavioural interactions

The effects of behaviour-mediated indirect interactions between predators and prey have been summarised by Heck and Valentine (2007), who termed them: 1) apparent competition, 2) apparent mutualism-facilitation, 3) exploitative competition and 4) trophic cascades. Apparent competition occurs when trophic interactions are amplified, such as when a more successful predator can reduce prey availability to a competing and less successful predator. Niche creation or expansion can occur through apparent mutualism-facilitation when prey is made available to new predators through behaviours designed to evade the more common predators (e.g. whales or tuna driving fish towards the surface where it becomes available to seabirds) (Ribic et al. 1997). Conversely, trophic interactions can be counteracted. For instance, removing tuna from a model including common fish prey and a competing seabird predator does not lead to increased seabird numbers, but causes seabird decline because the fish are no longer available without tuna driving them upwards (exploitative competition, Dill et al. 2003). Finally, behavioural trophic cascades can occur when a predator (e.g. dolphin) must change its preferred foraging habitat to evade another predator (e.g. tiger shark) and therefore transfers its predation effects to a habitat that would otherwise remain unaffected (Heithaus & Dill 2006).

Many indirect effects are mediated through behavioural modification of prey in response to predation or to the risk of predation (Heithaus et al. 2008a). Schooling species form tight aggregations near the surface to evade fish and cetacean predators, but in doing so they become available to seabird predators. Further indirect interactions based on behaviour include human fishers; when dolphins ‘corral’ tuna, aggregating around them to feed on them, this alerts human fishers to the presence of tuna, increasing the success of the predators (humans) but resulting in higher prey (tuna) mortality (Dill et al. 2003).

The most prominent example of behaviour-mediated indirect interactions in Australia has been documented in Western Australian waters. The high summertime abundance of dugong, sea snakes and sea turtles in Shark Bay attracts tiger sharks (*Galeocerdo cuvier*) to their preferred shallow foraging habitats (Heithaus 2001b; Heithaus & Dill 2006). The risk of predation by tiger sharks alters the behaviour of pied cormorants (*Phalacrocorax varius*), bottlenose dolphins (*Tursiops aduncus*), dugongs (*Dugong dugon*) and marine turtles (Heithaus & Dill 2006; Wirsing et al. 2007a). These species forgo favourable feeding habitat to reduce the risk of predation (Heithaus & Dill 2006; Heithaus et al. 2007a; Wirsing et al. 2007a); this interaction between sharks and their prey species may play an important role in structuring the overall Shark Bay seagrass community (Heithaus et al. 2007a). While tiger sharks have been identified as one of the most important apex predators on the GBR, evidence such as that gathered in Shark Bay is not available for GBR habitats.

Benthic Communities

Perhaps the least-known effect of predators of the GBR is the influence they may indirectly have on benthic communities. In a classic trophic cascade situation, predators indirectly affect plant communities by consuming herbivores (Pinnegar et al. 2000). This can also be applied across several trophic levels, and has been observed across a range of benthic marine ecosystems (Pinnegar et al. 2000). Direct evidence from temperate systems dominates this literature; while empirical studies from tropical marine ecosystems are much rarer. Some studies suggest a positive relationship between high predator densities and habitat-forming benthos. For instance, predator-dominated reefs in the Pacific were characterised by dominance of reef-building corals, as opposed to higher cover of macroalgae and soft corals on reefs where predators were depleted (Sandin et al. 2008). The studies reporting these effects took place on reefs also subjected to a gradient in pollution and nutrient input, suggesting an additional bottom-up effect acting on reef communities. Other studies found no flow-on effects of different densities of predators on benthic composition (Evans & Russ 2004;

Ayling & Choat 2008); however, a clearer benthic response may have resulted from a more detailed benthic sampling protocol. Studies from a Caribbean protected area reported a minimal effect of increased predator abundance on herbivory (Mumby et al. 2006). In this system, large-bodied parrotfish escape predation by the dominat reef predator, successfully removing macroalgae and facilitating coral recruitment (Mumby et al. 2007).

The most compelling cases for potential top-down effects of predators on the GBR is the recent evidence linking higher densities of predators to decreases in pests and diseases detrimental to corals. A significantly lower incidence (by a factor of 3.75) of the corallivorous starfish *Acanthaster planci* was found on coral reefs closed to fishing (Sweatman 2008). Similarly, a study on coral reefs in Fiji documented a significant relationship between a 61% decline in top predator densities, a three-orders of magnitude increase in starfish densities and a 35% decline in reef-building corals (Dulvy et al. 2004a). This starfish can populate reefs very quickly and decimate entire coral communities. Recent evidence suggests that the exploitation of predators can enhance this process, although the mechanism for this is unclear. It is suggested that the exploitation of common coral reef predators can result in a trophic cascade whereby decreased predation on invertebrate feeders can cause these to increase, in turn decreasing populations of invertebrates that prey on juvenile starfish (Sweatman 2008).

Outbreaks of coral disease are generally found to increase after disturbances or as part of the process of reef degradation (McClanahan et al. 2002). Recent work in the Philippines and on the GBR found a significant positive correlation between protection from fishing, higher functional diversity of coral reef fish and reduced prevalence of coral disease (Raymundo et al. 2009). The authors of this study hypothesise that butterflyfish (family Chaetodontidae), the only functional group positively associated with coral disease, may experience release from predation pressure in protected areas, and are also more abundant on lower-diversity reefs.

Economic Value

The GBRMP supports a range of industries and human activities. The primary economic benefits stem from tourism and commercial and recreational fisheries. It is difficult to calculate how much of this income is generated by predators, but they are highly valued by both industries.

Tourism

Tourism is the largest commercial activity in the GBRMP, contributing approximately $5.1 billion to the economy each year (Access Economics Pty Ltd 2008). Dive tourism on the GBR is heavily reliant on sites that offer aggregations of large predators, or that guarantee sightings of sharks (Chin & Kyne 2007). Surveys of SCUBA divers visiting the GBR found that sharks were rated as the most highly desired attraction (Miller 2005). The economic value of reef shark sightings has been calculated in other countries as in the tens of thousands of US dollars (Anderson 2002). At least one coral reef nation’s (the Maldives) diving tourism has declined as a direct result of the loss of sharks through overfishing (Anderson & Waheed 2002). Preliminay results of recent studies on tourism on the GBR show that people are willing to pay more for guaranteed sightings of some species, such as sharks and whales. In general, surveyed divers gave very high ratings to the experience of seeing sharks and large fishes, and out of 527 respondents, 165 (31.3%) particularly listed predators as desirable sightings (Birtles et al. 2008).

A study on the potential effect of reef degradation on numbers of visitors and associated tourism revenue for the GBR found that declines in coral and fish biodiversity could lead to drops in visitor numbers of as much as 80%. This decline would correspond to a loss of A$103 million in tourism revenue for the Cairns management area of the GBR alone (Kragt et al. 2009). Degraded reefs are generally associated with reduced fish diversity and smaller numbers of large fish (Fabricius et al. 2005). Large predators are therefore highly valued by the tourism industry. A simple calculation suggests that if a third of GBR tourists dive (Coghlan & Prideaux 2008), and a third of divers specifically expect to see predators (Birtles et al. 2008), then predators generate approximately $670 million per year for the tourism industry. However, this figure must be corroborated by targeted research before it can be used as a benchmark.

Fisheries

Fishing is the primary extractive activity occurring in the GBRMP, and has occurred for many decades (Little et al. 2005). Most of the fisheries operating in the GBR target predators (Robbins et al. 2006). There are five main commercial fisheries operating in the GBR with a total gross value estimated by different sources at between $114 and $251 million (Fenton et al. 2007; Oxford Economics 2009). The three largest fisheries operating within the GBRMP are the Coral Reef Finfish Fishery (CRFF), the East Coast Inshore Finfish Fishery (ECIFF) and the Trawl Fishery. Over 95% of reported commercial catches from the CRFF is taken from areas within the GBRMP (DPI&F 2007).

The CRFF is the largest reef-associated fishery in Australia and consists of three main sectors: a commercial sector, a charter fishing sector and a private recreational sector. All sectors use similar gears, typically single-baited hooks on heavy line with rod or hand reel. The fishery is multispecies in all sectors, but the primary targeted species is the common coral trout, *P. leopardus*. This fishery generates between $40 and $80 million per year in commercial sales and harvests approximately 125 species of mostly predatory fishes (Welch et al. 2008) – in the financial year 2007-2008, a gross value of production for the commercial sector of this fishery was estimated at $40 million (DEEDI 2009). *P. leopardus* and red throat emperor (*Lethrinus miniatus*) historically comprise approximately 70% and 15% of the annual commercial harvest, respectively (Mapstone et al. 2008). Since 2006, 90% of the coral trout catch has gone to supply the live fish market in Hong Kong. In the 2007-2008 financial year, the commercial coral trout catch was estimated at a little over 1,100 tonnes.

The second significant fishery in the GBRMP is the East Coast Inshore Finfish Fishery (ECIFF). This fishery includes commercial and recreational sectors, operates in tidal and nearshore waters and is primarily a net fishery. While a wide range of trophic levels of fishes are caught, this fishery targets a large number of coastal sharks – a total of 921 tonnes of shark were harvested in the 2007-2008 financial year, representing approximately 18% of the ECIFF's commercial catch. It is slightly smaller than the CRFF in terms of GVP, contributing approximately $24 million in the 2007-2008 financial year (DPI&F 2008c). A recent review suggests that mean effort has changed little over the last decade. As of July 2009, the catch of sharks by the commercial sector of Queensland east coast fisheries is restricted by a Total Allowable Catch (TAC) of 600 t (Gunn et al. 2008).

In addition, there are estimated to be 800,000 recreational fishers in Queensland with those using the GBR catching an estimated 3,500 to 4,500 tonnes of fish per year. Coral trout of the genus *Plectropomus* are the primary target for the recreational line fishery, as they are for the commercial sector. Recreational fishing, including both line and spearfishing, are culturally and economically important in many communities along the Great Barrier Reef coastline. Line fishing and spearfishing have approximately equal overall impacts on fishery resources per unit of fishing effort (Frisch et al. 2008). In 2008, the charter sector of the CRFF operated approximately 120 vessels in the GBRMP, mainly fishing midshelf and offshore reefs. Each vessel would take between 6 and 30 passengers for between 1 and 7 days (Mapstone et al. 2008). Collectively, the charter sector recorded a harvest of 346 tonnes in 2008.

Social and Cultural Value

Predators, especially sharks, have significant social and cultural significance in the GBRMP. The contribution of predators to tourism provides a strong indication of the iconic status of predators for those who seek a positive diving or snorkelling experience. Increasingly, the conservation of sharks and other large predators is becoming a priority for conservation groups; growing public awareness of shark exploitation is resulting in widespread concern and calls for protection (Rose & SAG 2001). Sharks are also important, both spiritually and socially, to indigenous groups inhabiting the GBR coast. Indigenous fishers consider fishing for shark a valuable activity in terms of providing food and increasing their social standing (Barnett & Ceccarelli 2007), and for several indigenous groups on the Queensland coast, sharks are totems and important characters in dreamtime stories (Chin & Kyne 2007).

RELATIVE IMPORTANCE OF PREDATORS ON THE GBR

The three groups of predators examined here are likely to play different roles at the scale of the whole GBR. While some apex predators may form seasonal aggregations for spawning or feeding purposes, such as tiger sharks converging at turtle nesting sites (Heithaus 2001b), or black marlin spawning aggregations (Pepperell & Davis 1999), their large size and food requirements means that they are likely to be widely dispersed, and therefore affect prey populations over large areas. Generalist top predators and high-level mesopredators are more likely to be relatively site-attached. They may have large home ranges or undetake ontogenetic habitat shifts or migrations (Ballagh et al. 2006; Heithaus et al. 2007b; Heupel et al. 2009a), but these two groups of species are likely to play a more localised role in GBR ecosystems. In calculating the importance index, the apex predators were therefore ranked separately from the other two groups. No strong distinctions exist between the generalist top predators and the high-level mesopredators and the division between these two groups is somewhat arbitrary. Although they are listed separately, these two groups were ranked together.

Apex Predators

Based on relative abundance, size and trophic level, tiger sharks are considered to be the most important apex predators in the GBR region (Table 4). While little is known of their biology and ecology on the GBR, satellite tagging studies have shown that they can move thousands of kilometres and utilise a wide range of habitats (Heithaus et al. 2007b). Research conducted elsewhwere suggest they structure prey and competitor communities that also occupy high trophic levels (Stevens et al. 2000). They may also control populations of cetaceans and turtles, especially during reproductively active times when they are most vulnerable (Heithaus et al. 2008b).

Other high-ranking apex predators include the wide-ranging and abundant bull shark, the oceanic swordfish and two hammerhead species, *Sphyrna mokarran* and *S. lewini.* Also ranked in the top 10 apex predators are the striped marlin, the pigeye shark (often confused with the very similar bull shark), the estuarine crocodile and the shortfin mako *Isurus oxyrinchus*. While these species are also large, often wide-ranging predators, they are likely to have their greatest effects in the specific environments where they are most abundant. The striped marlin and shortfin mako may be the most important oceanic predators in waters outside the GBR, and crocodiles play an apex role in inshore and estuarine waters. Species with the highest trophic rankings and the largest size, such as the orca and the white shark, have a potentially large impact when feeding in the GBRMP, but are too rare to be of very high importance overall.

Table 4. Rankings of relative abundance (whereby higher rankings reflect greater relative abundance), size (maximum total length) and trophic level used in calculating the importance index for species of apex predators on the GBR.

Species Common	**name**	**Habitat Abund**	**ance rank**	**Size rank**	**Trophic rank**	**Importance index**
Galeocerdo cuvier	Tiger shark	Inshore Reef Pelagic Deep water	12.00	9.00	12	1296.00
Carcharhinus leucas	Bull shark	Inshore Reef Pelagic Deep water	8.84	4.50	12	477.47
Xiphias gladius	Swordfish	Pelagic Deep water	5.05	6.83	8	275.87

Species	Common name	Habitat	Abundance rank	Size rank	Trophic rank	Importance index
Sphyrna leweni	Scalloped hammerhead	Inshore Reef Pelagic	4.42	5.25	10	232.11
Sphyrna mokarran	Great hammerhead	Inshore Reef Pelagic	1.01	9.00	12	110.96
Tetrapturus audax	Striped marlin	Pelagic Inshore	1.01	9.15	12	63.66
Carcharhinus amboinensis	Pigeye shark	Inshore Reef	1.26	6.30	10	53.05
Crocodylus porosus	Estuarine crocodile	Inshore Reef	0.38	4.20	10	40.93
Negaprion acutidens	Lemon shark	Inshore Reef	0.51	4.65	10	23.49
Isurus oxyrhinchus	Shortfin mako	Pelagic Reef	0.25	6.00	12	18.19
Orcinus orca	Orca	Pelagic Reef	0.13	12.00	12	18.19
Carcharhinus obscurus	Dusky shark	Inshore Reef Pelagic	0.25	5.48	12	16.60
Carcharhinus albimarginatus	Silvertip shark	Reef Pelagic	0.38	4.20	10	15.92
Carcharhinus falciformis	Silky shark	Pelagic Inshore	0.25	4.50	12	13.64
Carcharodon carcharias	White shark	Inshore Reef	0.13	9.00	12	13.64
Pseudorca crassidens	False killer whale	Pelagic	0.13	9.00	10	11.37
Isurus paucus	Longfin mako	Pelagic	0.13	6.45	12	9.78
Makaira mazara	Indo-Pacific blue marlin	Pelagic Inshore	0.13	7.50	10	9.47
Carcharhinus longimanus	Oceanic whitetip shark	Pelagic Reef	0.13	6.00	12	9.09
Makaira indica	Black marlin	Pelagic Inshore	0.13	6.98	10	8.81
Carcharias taurus	Greynurse shark	Inshore	0.13	4.80	10	6.06
Carcharhinus altimus	Bignose shark	Deep water Pelagic Inshore	0.13	4.50	10	5.68

Generalist Top Predators

The three abundant species of reef sharks, two very similar and abundant black tip sharks, and three large and abundant tuna species are included in the ten highest ranked species of generalist top predators. Also included in the top ten is the blue shark, a species that is probably the most abundant and wide-ranging of the shark species worldwide (Dulvy et al. 2008), and the spinner dolphin (Table 5). The only site-attached teleost reef predators to rank highly in the importance index are the common coral trout *P. leopardus* at number 13, and the larger bluespot coral trout *P. laevis* at number 22. The results of this importance index suggest that each of the broad GBR habitats has a unique suite of generalist top predators that locally define the nature and magnitude of predation pressure.

A large number of non-reef sharks are of intermediate to low importance according to the index, probably due to their relatively low abundance ranking. Many of these species are poorly known, and their distribution and abundance on the GBR is not well-documented. This is also true for some of the pelagic and deep-water predators on this list. Species that are low on the list should not necessarily be regarded as unimportant; greater knowledge could lead to large changes in their ranking, given the clustering of species in the mid to lower part of the table. Groupers of the genus *Epinephelus* are relatively rare, giving each species considered here a relatively low ranking. These species probably occupy a similar functional role, and collectively they may be more important than when each species is considered individually.

Table 5. Rankings of relative abundance, size (maximum total length) and trophic level used in calculating the importance index for species of generalist top predators on the GBR.

Species Common	**name**	**Habitat**	**Abundance rank**	**Size rank**	**Trophic rank**	**Importance index**
Triaenodon obesus	Whitetip reef shark	Reef	6.39	3.55	10	226.76
Thunnus albacares	Yellowfin tuna	Pelagic	6.71	3.98	8	213.87
Carcharhinus amblyrhinchos	Grey reef shark	Reef Inshore	5.20	3.75	10	194.89
Carcharhinus limbatus	Common blacktip shark	Inshore Pelagic	4.56	4.25	10	193.78
Stenella longirostris	Spinner dolphin	Reef Pelagic	4.81	3.92	10	188.22
Carcharhinus tilstoni	Australian blacktip shark	Inshore Pelagic	5.36	3.33	10	178.60
Thunnus obesus	Bigeye tuna	Pelagic	5.20	4.17	8	173.23
Prionace glauca	Blue shark	Pelagic	2.51	6.67	10	167.16
Thunnus alalunga	Albacore	Pelagic	8.20	2.33	8	153.10
Carcharhinus melanopterus	Blacktip reef shark	Inshore Reef	4.56	3.33	10	151.98
Carcharhinus brevipinna	Spinner shark	Inshore	3.88	3.88	10	150.68
Dalatias licha	Black shark	Deep water	4.81	3.03	10	145.77
Plectropomus leopardus	Common coral trout	Reef Inshore	12.00	2.00	6	144.01
Carcharhinus sorrah	Spot-tail shark	Inshore	5.20	2.67	10	138.59
Euthynnus affinis	Mackerel tuna	Pelagic	9.92	1.67	8	132.31
Sphyraena barracuda	Great barracuda	Reef Pelagic	5.97	3.67	6	131.24
Centrophorus niaukang	Taiwan gulper shark	Deep water	4.81	2.67	10	128.15
Sphyraena qenie	Blackfin barracuda	Reef Pelagic	7.02	2.83	6	119.36
Heptranchias perlo	Sharpnose sevengill shark	Deep water	4.81	2.33	10	112.13
Sousa chinensis	Indo-Pacific humpbacked	Inshore	3.88	4.57	6	106.31

Species Common	name	Habitat	Abundance rank	Size rank	Trophic rank	Importance index
	dolphin					
Sphyraena jello	Pickhandle barracuda	Reef Pelagic	7.02	2.50	6	105.32
Plectropomus laevis	Bluespotted coral trout	Reef	7.79	2.08	6	97.34
Delphinus delphis	Short-beaked common dolphin	Pelagic	2.51	3.87	10	96.96
Hemipristis elongata	Fossil shark	Inshore	2.51	3.83	10	96.12
Tursiops truncatus aduncus	Bottlenose dolphin	Inshore Reef	3.36	3.40	8	91.28
Scomberomorus commerson	Spanish mackerel	Pelagic	2.72	4.00	8	87.14
Acanthocybium solandri	Wahoo	Pelagic	2.51	4.17	8	83.58
Lutjanus bohar	Red bass	Reef	9.01	1.50	6	81.10
Centrophorus moluccensis	Endeavour dogfish	Deep water	4.81	1.67	10	80.09
Eusphyra blochii	Winghead shark	Inshore	4.26	3.10	6	79.25
Alopias superciliosus	Bigeye thresher	Pelagic	0.97	8.13	10	78.90
Scomberomorus semifasciatus	Grey mackerel	Inshore Pelagic	6.46	2.00	6	77.50
Squalus montalbani	Philippine spurdog	Deep water	4.81	1.58	10	76.09
Hexanchus makanurai	Bigeye sixgill shark	Deep water	2.51	3.00	10	75.22
Tetrapturus angustirostris	Shortbill spearfish	Pelagic	1.94	3.83	10	74.37
Mesoplodon pacificus	Longman's beaked whale	Pelagic	0.97	12.50	6	72.75
Globicephala melas	Long-finned pilot whale	Pelagic	0.97	12.00	6	69.84
Orcaella heinsohni	Australian snubfin dolphin	Inshore	2.51	4.58	6	68.96
Echinorhinus cookii	Prickly shark	Deep water	0.97	6.67	10	64.67
Carcharhinus plumbeus	Sandbar shark	Inshore	1.54	4.17	10	64.06
Carcharhinus cautus	Nervous shark	Inshore	2.51	2.50	10	62.69
Rhizoprionodon acutus	Milk shark	Inshore	4.26	1.83	8	62.49
Globicephala macrorhynchus	Short-finned pilot whale	Pelagic	0.97	9.82	6	57.13
Epinephelus fuscoguttatus	Flowery rockcod	Reef	4.61	2.00	6	55.35
Plectropomus maculatus	Barcheek coral trout	Inshore Reef	7.15	1.25	6	53.59
Squalus megalops	Spiked spurdog	Deep water	4.26	1.18	10	50.42
Glyphis glyphis	Speartooth shark	Inshore	0.97	5.00	10	48.50
Carcharhinus	Whitecheek	Inshore	4.26	1.37	8	46.58

Species	Common name	Habitat	Abundance rank	Size rank	Trophic rank	Importance index
dussumieri	shark					
Istiophorus platypterus	Sailfish	Inshore Pelagic	0.97	5.83	8	45.27
Carcharhinus fitzroyensis	Creek whaler	Inshore	1.94	2.25	10	43.65
Epinephelus lanceolatus	Queensland groper	Reef Inshore	0.97	4.50	10	43.65
Steno brendanensis	Rough-toothed dolphins	Pelagic	0.97	4.42	10	42.84
Rhizoprionodon taylori	Australian sharpnose shark	Inshore	3.88	1.17	8	36.21
Feresa attenuata	Pygmy killer whale	Pelagic	0.97	3.45	10	33.47
Gymnosarda unicolor	Dogtooth tuna	Reef Pelagic	0.97	4.13	8	32.08
Hypogaleus hyugaensis	Pencil shark	Inshore	2.51	2.12	6	31.84
Carcharhinus macloti	Hardnose shark	Inshore	2.51	1.42	8	28.42
Gempylus serpens	Snake mackerel	Deep water	1.94	1.67	8	25.87
Carcharhinus amblyrhynchoides	Graceful shark	Inshore	0.97	2.67	10	25.87
Ruvettus pretiosus	Oilfish	Deep water	0.97	3.00	8	23.28
Epinephelus malabaricus	Blackspotted rockcod	Reef Inshore	0.97	3.90	6	22.70
Epinephelus tukula	Potato rockcod	Reef	0.97	3.33	6	19.40
Thunnus tonggol	Longtail tuna	Pelagic	0.97	2.42	8	18.75
Epinephelus coioides	Goldspotted rockcod	Reef Inshore	1.54	2.00	6	18.45
Plectropomus areolatus	Passionfruit coral trout	Reef	2.25	1.25	6	16.89
Orectolobus maculatus	Spotted wobbegong	Reef	0.97	2.83	6	16.49
Epinephelus polyphekadion	Camouflage grouper	Reef	5.36	1.50	2	16.07

High-level mesopredators

Due to the difficulty in delineating generalist top predators and high-level mesopredators, the two groups were ranked together. The slightly lower trophic role performed by the high-level mesopredators is reflected in their lower overall importance rankings (Table 6). This group of predators, while perhaps less important on a large scale, nevertheless contains many trophically important species, especially for coral reefs (see also Table 2). Pelagic species such as trevallies, mahi mahi and mackerel are strongly represented in the top ten rankings in this group, along with the midwater pelagic gempylid *Lepidocybium flavobrunneum* and the giant moray *Gymnothorax javanicus*. The humphead Maori wrasse, *Cheilinus undulatus*, perhaps the most important predator of invertebrates on coral reefs, is ranked at number 10 in the high-level mesopredator group. Also represented on this list are a number of large and abundant predators of coral reef fish, including several species of snapper and the red-throat emperor *Lethrinus miniatus*.

Table 6. Rankings of relative abundance, size (maximum total length) and trophic level used in calculating the importance index for species of high-level mesopredators on the GBR.

Species	Common name	Habitat	Abundance rank	Size rank	Trophic rank	Importance index
Caranx ignobilis	Giant trevally	Pelagic Reef	5.50	2.83	10	155.90
Coryphaena hippurus	Mahi mahi	Pelagc	4.26	3.50	8	119.30
Lepidocybium flavobrunneum	Escolar	Deep water	4.26	3.33	8	113.62
Gymnothorax javanicus	Giant moray	Reef	3.36	4.50	6	90.60
Carangoides fulvoguttatus	Turrum	Pelagic Reef	7.42	2.00	6	89.06
Scomberomorus queenslandicus	School mackerel	Inshore Pelagic	7.42	1.67	6	74.22
Caranx melampygus	Bluefin trevally	Pelagic Reef	6.15	1.95	6	71.95
Katsuwonus pelamis	Skipjack tuna	Pelagic	3.88	1.83	8	56.91
Lutjanus malabaricus	Saddletail snapper	Inshore	5.50	1.67	6	55.02
Cheilinus undulatus	Humphead Maori wrasse	Reef	6.53	3.82	2	49.82
Epinephelus cyanopodus	Purple rockcod	Reef	3.69	2.00	6	44.32
Lutjanus argentimaculatus	Mangrove jack	Inshore Reef	4.26	2.50	4	42.61
Symphorus nematophorus	Chinamanfish	Reef	5.75	1.67	4	38.35
Variola louti	Yellowedge coronation trout	Reef	4.12	1.38	6	34.20
Aprion virescens	Green jobfish	Reef	4.26	1.87	4	31.81
Lethrinus miniatus	Redthroat emperor	Reef	9.28	1.50	2	27.85
Orectolobus ornatus	Ornate wobbegong	Inshore Reef	3.36	1.83	4	24.61
Eucrossorhinus dasypogon	Tasselled wobbegong	Reef	2.51	2.08	4	20.90
Lutjanus gibbus	Paddletail	Reef	9.32	0.83	2	15.54
Pseudocarcharias kamoharai	Crocodile shark	Deep water	0.97	1.83	8	14.23
Carangoides orthogrammus	Thicklip trevally	Pelagic	2.51	0.83	6	12.54
Hemigaleus australiensis	Australian weasel shark	Inshore	0.97	1.83	6	10.67
Lutjanus monostigma	Onespot snapper	Reef	5.20	1.00	2	10.39
Caranx lugubris	Black trevally	Pelagic Reef	0.97	1.67	6	9.70
Lutjanus rivulatus	Maori snapper	Reef	2.72	1.12	2	6.08
Caranx papuensis	Brassy trevally	Pelagic Reef	0.97	1.47	4	5.69

Relative to other functional groups in marine ecosystems, apex predators are credited with maintaining ecosystem health (Robbins et al. 2006), although the mechanisms by which they do this are not well understood and empirical evidence is still largely lacking. The interactions between the three groups described above, whereby there can be competition and predation both between and within the three groups, are complex and have been described only for few species or species groups. For instance, Stallings (2008) documented how large predators indirectly effected an increase in prey recruitment by causing reduced feeding activity in mesopredators – but the large predators in his study – large groupers – can themselves fall prey to larger sharks. These larger predators – those included in the apex group in this study – therefore potentially regulate prey abundance, diversity, species composition and behaviour throughout the other two levels and beyond. It is expected that the largest and most mobile predators can trophically link spatially separated food webs and habitats (Ings et al. 2009). The presence of healthy predator populations from all three functional groups is expected to prevent the dominance of space and energy by a few competitively superior species and, by thus promoting biodiversity, to enhance resilience (McCann 2007).

STATUS AND EXPLOITATION LEVELS OF GBR APEX PREDATORS

Status: Threats and Vulnerability

Overall, at least 26 of the predators identified here are protected under State, Federal and / or international legislation (

Table 7). Most of the protected species are elasmobranchs or cetaceans, as their life histories and the relative rarity of the individual species make them most vulnerable to human impacts. The humphead Maori wrasse and three species of grouper are also protected; late-maturing, long-lived teleosts are increasingly recognised as in need of protection (e.g. Marriott et al. 2007).

Table 7. Status of GBR predators under State, Federal and international legislation. International Union for the Conservation of Nature (IUCN) categories: Vu: Vulnerable; En: Endangered. *Environment Protection and Nature Conservation Act 1999* (EPBC) categories: CE: Critically Endangered; Vu: Vulnerable; Cet: listed Cetacean; Mar: listed Marine. Other – Queensland *Nature Conservation Act 1992* (QNCA) category: T: Threatened; Bonn: listed under The Convention on the Conservation of Migratory Species of Wild Animals.

Family Species		**Common Name**	**IUCN**	**EPBC**	**Other**
Carcharhinidae	*Carcharhinus longimanus*	Oceanic whitetip shark	Vu		
Carcharhinidae	*Carcharias taurus*	Greynurse shark	Vu	CE	QNCA (T)
Carcharhinidae	*Glyphis glyphis*	Speartooth shark		CE	
Carcharhinidae	*Negaprion acutidens*	Lemon shark	Vu		
Centrophoridae	*Centrophorus niaukang*	Taiwan gulper shark	Vu		
Centrophoridae	*Centrophorus moluccensis*	Endeavour dogfish	En		
Lamnidae	*Isurus paucus*	Longfin mako shark	Vu		Bonn
Lamnidae	*Isurus oxyrinchus*	Shortfin mako shark	Vu		Bonn
Orectolobidae	*Orectolobus maculatus*	Spotted wobbegong	Vu		
Hemigaleidae	*Hemipristis elongata*	Fossil shark	Vu		
Lamnidae	*Carcharodon carcharias*	White shark	Vu	Vu	Bonn
Squalidae	*Squalus montalbani*	Philippine spurdog	En		
Delphinidae	*Delphinus delphis*	Short-beaked common dolphin		Cet	
Delphinidae	*Feresa attenuata*	Pygmy killer whale		Cet	
Delphinidae	*Globicephala macrorhynchus*	Short-finned pilot whale		Cet	
Delphinidae	*Globicephala melas*	Long-finned pilot whale		Cet	
Delphinidae	*Orcaella heinsohni*	Australian snubfin dolphin		Cet	Bonn
Delphinidae	*Orcinus orca*	Orca		Cet	Bonn
Delphinidae	*Pseudorca crassidens*	False killer whale		Cet	
Delphinidae	*Sousa chinensis*	Indo-Pacific		Cet	Bonn

Family Species		Common Name	IUCN	EPBC	Other
		humpbacked dolphin			
Delphinidae	*Stenella longirostris*	Spinner dolphin		Cet	
Delphinidae	*Tursiops truncatus aduncus*	Bottlenose dolphin		Cet	
Crocodylidae	*Crocodylus porosus*	Estuarine crocodile		Mar	Bonn
Labridae	*Cheilinus undulatus*	Humphead Maori wrasse	En		
Serranidae	*Epinephelus lanceolatus*	Queensland groper	Vu		
Serranidae	*Plectropomus areolatus*	Passionfruit coral trout	Vu		
Serranidae	*Plectropomus laevis*	Bluespotted coral trout	Vu		

The two predominant threats to GBR predators are overexploitation and habitat degradation (Wilson et al. 2008). It is now well-documented that predators are the most heavily exploited of marine organisms (Myers et al. 2007). The collapse of fisheries targeting large-bodied, long-lived predatory teleosts and elasmobranchs suggests that it is unlikely that many predators can be sustainably harvested at a commercially viable level without strict management (Walker 1998). The degradation of GBR ecosystem by human activities, from extractive industries to the effects on water quality, can further affect populations of predators, either directly by reducing the quality of their habitat, or indirectly by affecting the abundance and availability of prey (Chin & Kyne 2007). However, there is considerable variability in the life-history, abundance and distribution of the GBR's predators. Different species are therefore subjected to different types of threats and display different levels of vulnerability.

Each category of predators considered in this review contains a number of species subject to some level of exploitation or direct impact (e.g. by-catch or shark control catch). There are 19 species of apex predators (83% of total), 54 species of generalist top predators (81%) and 23 species of high-level mesopredators (88%) currently known to be caught, either as target species or incidentally.

Fisheries

Most fishing in the GBR region tends to target large-bodied, predatory fish species. As these larger predators are depleted, fisheries increasingly target species of lower trophic levels – a phenomenon termed 'fishing down marine food chains' (Pauly & Palomares 2005). Compared with other marine regions world-wide, fisheries on the GBR are relatively light and selective (FAO 2008), making the fishing down of marine food chains less likely or severe. Human exploitation has depleted marine fish biodiversity and altered fish community structure on a large scale (Hutchings & Baum 2005). The history of tropical fisheries management indicates that management efforts are often instigated after exploitation has peaked, and the fisheries are left with very reduced stocks (Myers & Worm 2003). Unfortunately, official catch statistics do not take into account the fish biomass lost to poaching or ghostfishing by lost or abandoned fishing gear, and data on recreational fishing can be unreliable (Dayton 1998).

The major effects of fishing on ecosystems include (1) changes in habitat due to physical disturbance associated with fishing operations – especially towed gears; (2) by-catch – ie. catch that is discarded, affecting mortality rates of by-catch species and the effects of the discards on the environment; (3) changes in the balance between trophic levels, expressed by the relative abundance of predators and their prey; (4) changes in competitive interactions among species; (5) changes in diversity and community structure; and (6) the effects on the ecosystem of lost fishing gear (Goni 1998; Ley et al. 2002). All these impacts have the potential to affect predator populations, their prey, and the ecosystems they depend on.

Globally, it has been estimated that marine fisheries have declined by approximately 0.7 million tonnes per year since the 1980s, with at least 28% of the world's stocks severely depleted and another 52% fully exploited by 2008 (FAO 2008; Mora et al. 2009). Compared to other marine regions of the world, Australian stocks are considered at low risk of overexploitation (Coll et al. 2008; FAO 2008). Only 2% of the world's coral reefs are protected in Marine Protected Areas (MPAs) that are considered adequate for the full protection of those reefs (Mora et al. 2006). In this context, Australia is considered to be a leading nation, with 69% of regional reefs included in networks of multipurpose and / or no-take MPAs (Mora et al. 2006). Compared to the Caribbean, for instance, the GBR hosts roughly 2.5 times the number of large carnivorous species (Bellwood et al. 2004). However, it is important to note that despite its large area, the Australian fishing zone is relatively unproductive, with nutrient-poor waters (Lowe et al. 2003).

Elsewhere in the world, it has been estimated that industrialised fishing depletes biomass at a rate of approximately 16% per year, resulting in an overall decline of 80% within 15 years (Myers et al. 1997). Once depleted, the fisheries themselves are subject to a relatively low yield for a given level of fishing effort (Marriott et al. 2007). Furthermore, as shifting baselines lead to the taking of smaller individuals, these are less able to contribute to future recruitment, hastening the collapse of the population (Crouse 1999; Myers & Worm 2003). How this may be applicable on the GBR is unknown. Systems with lower diversity are expected to suffer greater degradation, and sometimes phase shifts, once large predators are lost (Bellwood et al. 2004). So far, the establishment of well-policed MPAs has been the best protection for large-bodied predators (Robbins et al. 2006).

Vulnerability to overexploitation:

Most of the GBR's apex predators have life histories that include late maturation, slow growth, low fecundity, a long life expectancy and a tendency to form spawning aggregations (Russell 2001; Chin & Kyne 2007). Animals with these characteristics are especially prone to overexploitation (Pears et al. 2007), and depleted populations take a long time to recover (Myers & Worm 2003; DeMartini et al. 2008). The vulnerability of apex predators to overexploitation is highlighted by the documented depletion and collapse of fisheries worldwide (Walker 1998). Recent research has revealed significant declines in populations of whitetip reef sharks, *Triaenodon obesus*, and grey reef sharks, *Carcharinus amblyrhynchos*, on the GBR (Robbins et al. 2006). The shark fin trade, which is still largely unregulated, poses the greatest threat to shark populations world-wide (Clarke et al. 2006). A further source of regional shark mortality stems from drumlines in the Queensland shark control program (Dudley et al. 1998).

A number of the GBR's predator species are known to form spawning aggregations, including *Cheilinus undulatus*, *Lethrinus miniatus*, *Aprion virescens*, *Lutjanus bohar*, *L. argentimaculatus*, *Symphorus nematophorus*, *Scomberomorus commerson*, *Epinephelus fuscoguttatus*, *E. malabaricus*, *E. polyphekadion* and *Plectropomus* spp. Of the species considered here, 16.6% (11) of the generalist top predators and 36% (9) of the high-level mesopredators have been recorded as forming spawning aggregations on the GBR and elsewhere (Russell 2001). In some cases, these aggregations are targeted by fishers, because they offer the opportunity to exploit numerous large individuals in a relatively short period (Sadvoy & Domeier 2005; Pears et al. 2007). This has especially been corroborated for large groupers, such as *Epinephelus fuscoguttatus* and *E. polyphekadion* (Pears 2005).

The fishing of spawning aggregations is widely known to be destructive to fish stocks and has been implicated in the decline or disappearance of aggregation spawning species elsewhere in the world (Sadovy & Domeier 2005). The threat of this practice to GBR predators has been recognised (Russell 2001). Spawning aggregations are a significant contribution to the next generation of these species and require protection to safeguard against severe stock depletion (Russell 2001). Sadovy and Domeier (2005) wrote that “Available data and analyses of aggregation-fisheries and aggregating species strongly suggest that: (1) the majority of known aggregations that are exploited are yielding declining landings; (2) aggregating species show greatest overall declines in local fisheries when their aggregations are also exploited; (3) from an economic perspective, aggregation fishing may yield lower prices for fish, or aggregations may be more valuable unexploited, as a source of fish for local fisheries or as tourist attractions; (4) hyperstability can mask declines in aggregation fisheries, based on fishery-dependent data; (5) monitoring of aggregation catches by either fishery-dependent or fishery-independent means is deceptively challenging.”

By-catch

Large numbers of species, including apex predators, are incidentally killed as ‘by-catch’, which is often discarded and not usually included in catch statistics (Dayton 1998). On the GBR, all fisheries result in a certain level of by-catch, harvest (dive-based) fisheries excepted (Frisch et al. 2008). Stock assessments generally don’t account for discarded catch, making it difficult to estimate the effect of by-catch on populations (Welch et al. 2008). Overall by-catch in the ECIFF ranges between 20 and 28% (Halliday et al. 2001) and in recreational line and spear fisheries by-catch has been recorded at 65% (Frisch et al. 2008). The proportion of and species composition of predators that are discarded varies for different fisheries. Annual discard rates between 1989 and 2003 of the CRFF amounted to 292–622t and 33–95t for coral trout and red throat emperor respectively (Welch et al. 2008). It was expected that the management changes of 2003-2004 would result in higher discard rates as a result of more stringent individual size and bag limits (Welch et al. 2008). The ETBF longline fisheries targets tuna and billfish and while it does not operate inside the GBRMP, it is highly likely to affect offshore pelagic GBR species. Over 100 marine species have been recorded from the ETBF catch, including fish, sharks, seabirds, turtles and cetaceans (DEWHA 2008). It is estimated that 30-50% of the total recreational catch in Australia is discarded (Henry & Lyle 2003). By-catch discards are then eaten by scavengers and opportunistic predators, and can result in consistent aggregations of sharks, dolphins and seabirds in heavily fished areas (Stevens et al. 2000).

Most information on the amount and survival rates of by-catch comes from trawl fisheries (Welch et al. 2008), probably because this gear type causes the greatest amount of by-catch (Goni 1998). The amount and species composition of by-catch varies according to target species, mesh size, habitat and environmental conditions (Halliday et al. 2001). The highest volume of by-catch results from prawn trawling; it is estimated that Australia’s Northern Prawn Fishery catches 56 elasmobranch species from 16 families (Stobutzki et al. 2002). This study found that *Carcharhinus tilstoni*, *C. dussumieri*, *Rhynchobatus djiddensis* and *Himantura toshi* represented 65% of the by-catch in number per km trawled. For most species, over 50% of individuals in the by-catch were immature. For all species combined 66% of by-catch individuals died in the trawl net. Less than 20% of the GBRMP is trawled commercially (Figure 9), with less than 10% actually trawled more than once per year between 2002 and 2005 (Coles et al. 2008). The trawl fishery in the GBR is not permitted to retain predators, and bycatch reduction devices and turtle excluder devices are compulsory. However, some bycatch issues remain for predators, with sharks forming a relatively small but potentiallt ecologically significant component of bycatch in the fishery (Kyne et al. 2002).

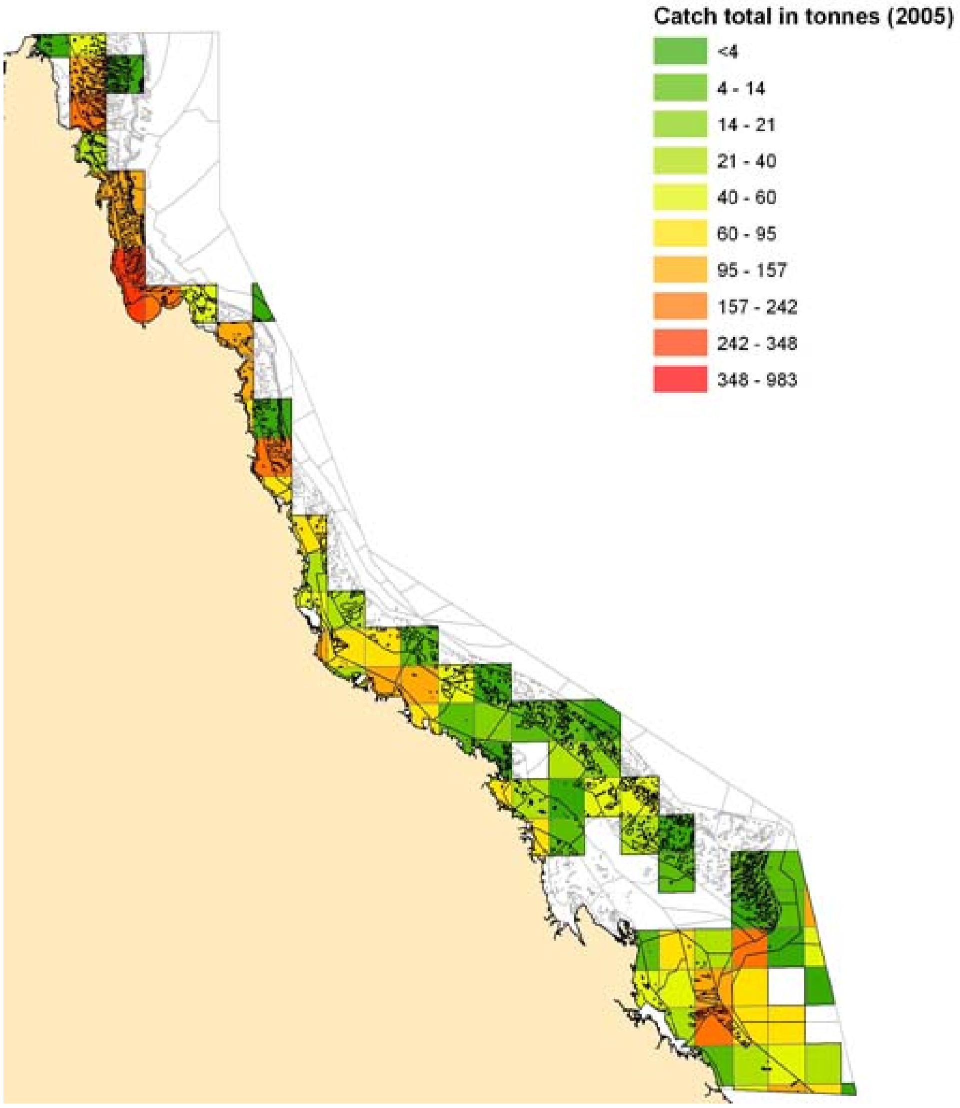


Figure 9. Total areas trawled by Queensland's commercial trawl fisheries in 2005, with catch in tonnes. Data from QPIF.

Post-release mortality and sub-lethal effects

Many recreational fishers release caught fish, either to avoid unnecessarily depleting fish populations, or to comply with size limits. Bartholomew and Bohnsack (2005) reviewed post-release mortality for a number of species targeted by the American sportfishing industry. A number of factors were important determinants of mortality rates in large predatory fish, including hooking location, depth, fish size, hook type and handling. Fish hauled rapidly from deeper water can experience barotraumas with loss of swim bladder function. The release of gas from overinflated swim bladders with a hypodermic needle, known as 'venting', has variable effects on the fish depending on the experience of the handler and can lead to death (Nguyen et al. 2009). Indirect mortality through post-release predation and sub-lethal effects is less well-documented, and can be significant. Vulnerability to predation during capture and directly after release can result in mortality rates as high as 20%, and sub-lethal post-release effects can include reduced growth and reproductive rates, nest abandonment and a decline in nest guarding activities (Broadhurst et al. 2005). Reported catch rates do not include post-release mortality, especially of discarded catch (Bartholomew & Bohnsack 2005).

For reef fish species on the GBR, it is estimated that post-release mortality is 15-20% (Mapstone et al. 2008). The fate of released individuals is of high importance, especially in those fisheries with high release rates (McLeay et al. 2002; Heupel & Simpfendorfer 2008). General guidelines suggested for the protection of fishes from post-release effects include minimising the duration of fishing activities, minimising air exposure once a fish is caught, avoiding water temperature extremes, the use of barbless hooks and artificial lures, and avoiding spawning aggregations and reproductive periods (Cooke & Suski 2005).

Broadhurst et al. (2005) showed that mortality can be delayed after release, increasing the difficulty in assessing post-release mortality where individuals are not followed by tagging or restraining in sea cages. Through estimates obtained during their study, they determined that annual short term release mortalities of just two of the popular species caught by recreational fishers in inshore habitats (yellowfin bream and snapper) could be as high as 2.3 and 0.8 million individuals, respectively.

Fisheries Management and GBRMP Zoning

Ideally, fisheries are managed based on robust scientific data that takes into account both the stocks of the targeted species and the status of the ecosystem (Mora et al. 2009). When there is uncertainty, however, the precautionary principle must be applied (Pikitch et al. 2004). Increasingly, there is acknowledgement of the effect of fishing activities on non-target species, such as habitat destruction, by-catch and post-release mortality, evolutionary shifts in population demographics, and changes in the structure and functioning of ecosystems (Pinnegar et al. 2000; Pikitch et al. 2004). In reality, however, fisheries management traditionally focuses exclusively on target species, and decisions are aimed at a relatively short timeframe of between 1 and 5 years (Mapstone et al. 2008). It has tended to be reactive rather than proactive, with predictions of future stock status based on analyses of past catches. This approach can be at odds with the goals of management for biodiversity conservation (Mapstone et al. 2008).

Using marine reserves as fisheries management tools has proven successful for the protection of target species (Mapstone et al. 2008). Besides safeguarding target populations within their boundaries, marine reserves have been shown to benefit overall biodiversity (Jones et al. 2007), as well as neighbouring fisheries through the spill-over of larvae and adults (Roberts et al. 2001). Even when MPAs are designed to protect biodiversity, their primary effect is the inhibition of extractive activities such as fishing (Little et al. 2005).

For MPAs to be effective, there must be good compliance with fishing closures, and they must be self-seeding or connected via recruitment to other MPAs or sources of larvae. Recent work in Papua New Guinea has shown that both processes can co-occur (Planes et al. 2008), and DNA analyses are underway to show connectivity for protected zones of the GBR. However, the remoteness of some parts of the GBR can be an obstacle, as shown by a study on illegal trawling in closed parts of the northern GBR, where it was estimated that 3,260 illegal trawling days occurred annually in the late 1990s (Gribble & Robertson 1998).

The GBRMP is managed for multiple use, with 33% of its area closed to fishing. However, closures to fishing are only successful if they are effectively enforced. Fishing regulations are often met with protests from the fishing community (Dayton 1998; Shertzer & Prager 2007), and surveillance in an area as large as the GBRMP is costly and logistically difficult (Davis et al. 2004; Williamson et al. 2004). Comparisons of heavily and lightly fished zones can serve to illustrate the effects of fishing on the GBR (Bellwood et al. 2004). Using green (no-take) zones as 'no fishing' comparisons may be problematic, as recent work has shown some variability in compliance (Davis et al. 2004). Robbins (2006) considered that there is a gradient in actual protection level on the GBR, using the most basic distinctions of Blue (open to fishing), Green (closed to fishing but otherwise open to entry) and Pink (aerially surveyed, strictly enforced exclusion areas) Zones. Even the relatively moderate levels of illegal fishing in Green Zones (Davis et al. 2004) has resulted in a significant decline in populations of sharks and large serranids when compared with Pink Zones (Robbins et al. 2006; Ayling & Choat 2008). Comparing Pink Zones with Blue (open to fishing) Zones indicated a decline of whitetip reef sharks and grey reef sharks of up to 80% and 95%, respectively (Robbins et al. 2006).

Perhaps the largest body of research concerning predators on the GBR are the studies on the effects of fishing on individual predator species that are targeted by fisheries operating within the GBR. No-take areas have been found to be highly effective in increasing the abundance, size and biomass of exploited generalist top predators, such as *P. leopardus* (Graham et al. 2003; Cappo et al. 2009). Studies conducted on the GBR and elsewhere corroborate the positive effect of no-take areas on exploited species (Russ & Alcala 1996; Bohnsack 1998; Graham et al. 2003; Halpern 2003). Overall ecosystem effects of protecting predators from fishing are less well documented.

While the effects of protection from fishing can readily be measured for relatively sedentary predators (usually in the generalist top predator category), they are more difficult to detect for large, wide-ranging apex predators such as large sharks. Chapman et al. (2009) argue that research on the effects of sharks on overall marine reserve ecosystem health is equivocal, and that there is a need for comparative research on marine reserves with and without large populations of sharks. Despite background shark predation, marine reserves can support increased densities of both intermediate predators (e.g. groupers) and large grazers (e.g. parrotfish) (Mumby et al. 2009). A comparison of estuaries open and closed to fishing adjacent to the GBRMP found that closed estuaries supported greater numbers of large predators (including bull sharks and Spanish mackerel), and that this did not correlate with a decline in prey species (Ley et al. 2002). This may be due to the large biomass of by-catch caught by net and trawl fisheries in inshore areas of the GBR, directly depleting prey species as well as predators (Ley et al. 2002).

Habitat Degradation

Human activities affect marine habitats of the GBR in a variety of ways. Inshore and coastal waters are perhaps the most heavily impacted of the GBR's habitats, as run-off carrying sediment, pollutants and nutrients flows directly into coastal waters. Direct human impacts, including exploitation through fisheries, are also more concentrated in nearshore areas due to their greater accessibility. Future impacts such as increased erosion, temperature and salinity fluctuation and direct human use are expected to increase most rapidly in this habitat (Sheaves et al. 2007). Inshore soft-bottom habitats on the GBR are likely to have suffered the effects of bottom trawling and, to a lesser degree, net fisheries. Coral reefs are also affected by land-based and direct extractive anthropogenic activities, with a distinct cross-shelf gradient in land-based influence.

Coral reefs are also expected to be most vulnerable to the increasing temperatures and acidification predicted under future climate change (Hughes et al. 2003). Offshore pelagic and deep-water habitats are perhaps the least vulnerable habitats, although changes in currents and productivity, changing temperature regimes and the large-scale exploitation of many species through industrial longlining can also degrade these habitats (Kingsford & Welch 2007).

Top predators are easily affected by conditions of habitat loss, degradation or fragmentation. For instance, water temperatures and salinity changes can play a role in the movements of bull sharks and their prey in estuaries (Ortega et al. 2009). However, wide-ranging species and those species and groups already subject to a wide range of conditions are likely to be the least vulnerable to shifts in environmental parameters.The destruction or removal of sessile organisms that give the habitat its structural complexity is highly likely to affect communities using those habitats (Pinnegar et al. 2000). Apex predators are likely to be affected indirectly through prey species that may decline as a result of habitat loss. For instance, Caribbean fishes of all trophic levels are responding negatively to habitat degradation (Paddack et al. 2009). Under increased anthropogenic pressures on marine habitats, the structure of coral reef fish communities is expected to change (Wilson et al. 2006). Large predators are also likely to directly respond to the loss of structural complexity, for example through severe tropical storms (Wilson et al. 2006).

Exploitation Levels

Almost all the species of predators considered in this review are under some level of exploitation on the GBR. Due to inconsistencies in the level of species identification, the three categories of predators must often be considered together in terms of their exploitation levels. Many are targeted by the two primary GBR fisheries, the CRFF and the ECIFF, and others are by-catch or caught in Queensland's Shark Control Program. Larger, oceanic species that use GBR habitats are also caught in the ETBF longlines. In fact, human exploitation is the primary factor threatening large predators in many ecosystems (Duffy 2003).

Fisheries of the GBR are under different forms of management, from size limits and TAC to area and seasonal closures through Marine Park zoning. There is some disagreement about the level of sustainability of some species caught by these fisheries. For instance, it was considered by many managers, stakeholders and researchers that the CRFF was fully exploited at 1996 effort levels; and effort nevertheless increased by 35% in subsequent years before a TAC at 1996 levels was introduced (DEH 2005). Individual species and species groups of predators are subject to different levels of exploitation, and the specific life-history characteristics and habitat requirements of each group affect their vulnerability to overexploitation.

Sharks

Fisheries catch

In 2007, 921 tonnes of sharks were recorded as catch by the ECIFF alone (DPI&F 2008b). It is not possible to ascertain the exact species composition of captured sharks, as identification practices are poor (Gunn et al. 2008). Where species were recorded, it was reported that 11.6 tonnes of bull sharks (*Carcharhinus leucas*) were caught in the commercial net fisheries between 2005 and 2008, and 226.8 tonnes of scalloped hammerhead (*Sphyrna lewini*) were caught by the net and charter fisheries combined over the same period. Due to the confidentiality issues with releasing data collected from less than five vessels, however, there is some uncertainty in these estimates.

Recreational catch data from 2005 shows a shark catch of 106,449 individuals for the GBRMP regions, of which 93,376 (87.7%) were released. The mortality rate of released sharks is unknown, but it is likely that the estimated retained catch of 13,074 sharks is an underestimate of the actual mortality incurred by sharks in 2005. Combining information from commercial and recreational fisheries and the Queensland Shark Control Program is problematic, because commercial fisheries report catch (and sometimes by-catch) in weight measurements, while other sources of shark mortality record numbers of individuals.

The harvesting of sharks, both as target and by-catch, has been examined with varying conclusions about the sustainability of these fisheries. Studies have focused either on wide-ranging species or on more site-attached, reef-specific species such as grey reef sharks and whitetip reef sharks (Robbins et al. 2006). Site-attached species may be more vulnerable to overexploitation and declines in habitat quality (Heupel et al. 2009b). Almost all sharks have low maximum intrinsic rates of population increase, with recruitment directly related to existing stock (Walker 1998), and once their numbers are severely depleted, recovery is expected to be very slow (Baum et al. 2003).

On the Hong Kong shark fin market, tiger sharks comprised 0.08 to 0.19% of the trade, while more commonly traded carcharhinid sharks included the blue (17.3%), silky (3.5%), sandbar (2.4%), and bull (2.2%) sharks (Clarke et al. 2006). It is unknown what proportion of the shark fin trade is comprised of Australian sharks, or sharks caught and finned in the GBRMP. New management practices and a national ban on shark finning in the tuna industry caused decreased shark catches by the CRFF in 2003 (Heupel et al. 2009b). However, it was also noted that incidental shark catches have often gone unidentified, misidentified or unreported by as much as 10-40% (Walsh et al. 2002). It was also estimated that 2.2 times as many sharks are encountered and then lost or released than are brought on board, but the fate of hooked and lost or released individuals is unknown (Walsh et al. 2002).

In the GBRMP, the ECIFF is the primary fishery directly targeting sharks. The sharks most commonly caught by the fishery are black-tip sharks (*Carcharhinus tilstoni* and *C. limbatus*), milk shark (*Rhizopriondon acutus*) and scalloped hammerhead shark (*Sphyrna lewini*) (Tobin 2009). Sharks are generally not subject to specific fishery limits (Robbins et al. 2006), and this is certainly the case within the ECIFF (DEH 2005). An independent review of the ECIFF expressed concern at the proposed TAC of 700t being set despite the general lack of knowledge about biology, ecology and distribution of a number of the commonly caught shark species (Gunn et al. 2008). A preliminary vulnerability assessment found that there was some variability in the sustainability of the individual shark species harvested by the ECIFF. However, this assessment showed that except for three species (blacktip reef shark *Carcharhinus melanopterus*, Australian sharpnose shark *Rhizoprionodon taylori* and Australian cownose ray *Rhinoptera neglecta*), all the species harvested were ranked between the medium and high risk mark (Gribble et al. 2005).

By-catch

A recent study found a high level of shark by-catch in the CRFF (Heupel et al. 2009b). Data were collected from three sources: fishery logbooks, an observer program within the fishery and a fishery-independent survey. Catch rates of identified sharks were comprised primarily of grey reef (62–72%), whitetip reef (16–29%) and blacktip reef (6–13%) sharks. No increase or decline in shark catch per unit effort was observed over the period between 1989 and 2006. Higher catch per unit effort in no-take Green Zones indicated that these areas are effective at protecting a portion of the reef shark population from exploitation (Heupel et al. 2009b).

It is reported that Australia's Northern Prawn Fishery regularly catches 56 elasmobranch species from 16 families as by-catch (Stobutzki et al. 2002). Sharks and rays caught as by-catch were often immature and two-thirds were recorded as dying in the trawl net. The survival rates of individuals that were released alive is unknown. While much research has focused on minimising the impact of trawling on cetaceans and reptiles, the effects of trawling on shark populations of the GBR is largely unknown.

Queensland Shark Control Program

Between 1997 and 2008, 7,082 sharks have been caught in Queensland's shark control programs, which consist of either mesh netting or baited drumlines set offshore from popular swimming beaches. This equates to an average of approximately 643 sharks per year along Queensland's east coast; approximately 64% (4,509 individuals) of the total catch is from within GBRMP waters. The Mackay area records the highest average annual catch of sharks larger than 2m in length with nearly 70 sharks per year; between 30 and 40 sharks a year are caught in the Capricorn Coast, Cairns, Townsville and Bundaberg areas and 11 in Tannum Sands off Gladstone (Figure 10).

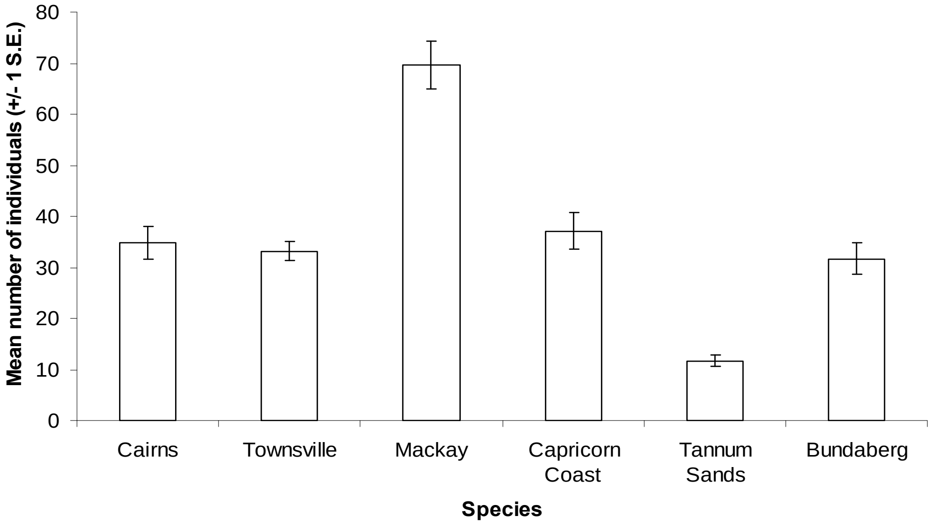


Figure 10. Mean annual catch (+/- 1 S.E.) between 1997 and 2008 of sharks larger than 2m in length within the GBRMP.

Over the entire Queensland coast, most of the sharks caught were tiger sharks (*Galeocerdo cuvier*); these were, on average, twice as abundant in the shark catch as the next most abundant species (bull shark *Carcharhinus leucas*) (Figure 11). Most tiger sharks were caught off Mackay; 505 individuals were recorded there between 1996 and 2006, while 231, 279, 250 and 81 were recorded from Cairns, Townsville, the Capricorn Coast and Gladstone, respectively (Appendix 1). Other sharks caught regularly, at an average of between 38 and 62 sharks per year, are blacktip sharks (assumed to be a combination of *C. limbatus* and *C.tilstoni),* bignose sharks (*C.altimus*), other whaler sharks (family Carcharhinidae) and scalloped hammerheads, *Sphyrna lewini*. Even small numbers of species

considered oceanic have been recorded on these inshore drumlines (e.g. silky and mako sharks), suggesting either an error in species identification, or the need to review current knowledge about the habitat preferences and distributions of some species. Overall, shark catches have remained stable over the ten years of record-keeping (

Figure 12).

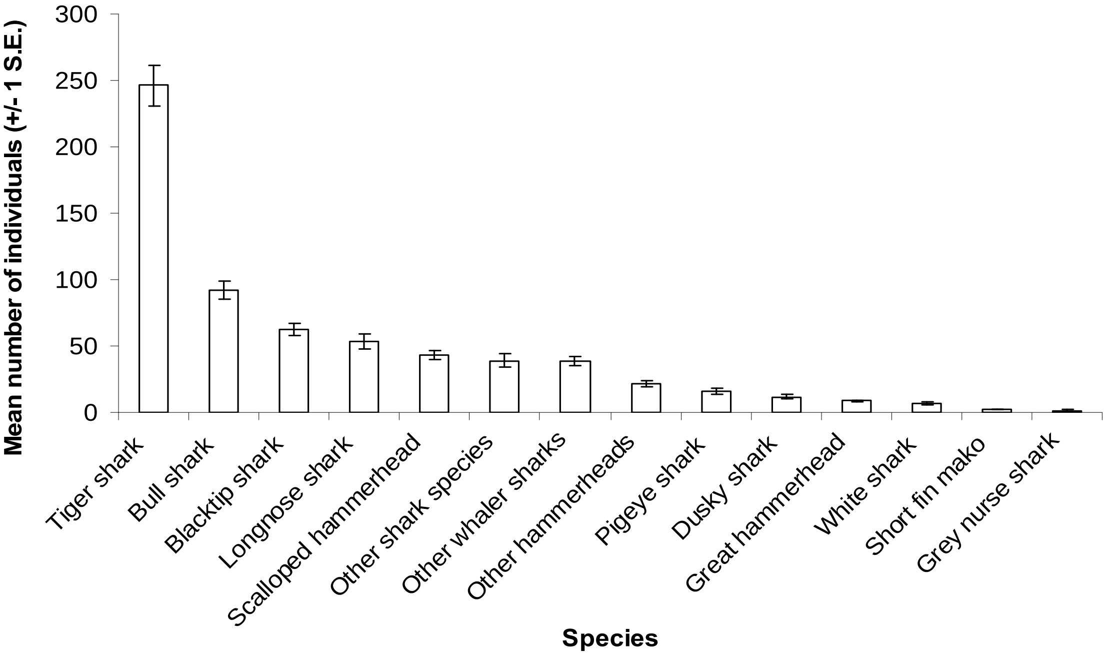


Figure 11. Mean number of individual sharks (+/- 1 S.E.) of each identified species caught in Queensland's shark control program between 1997 and 2008.

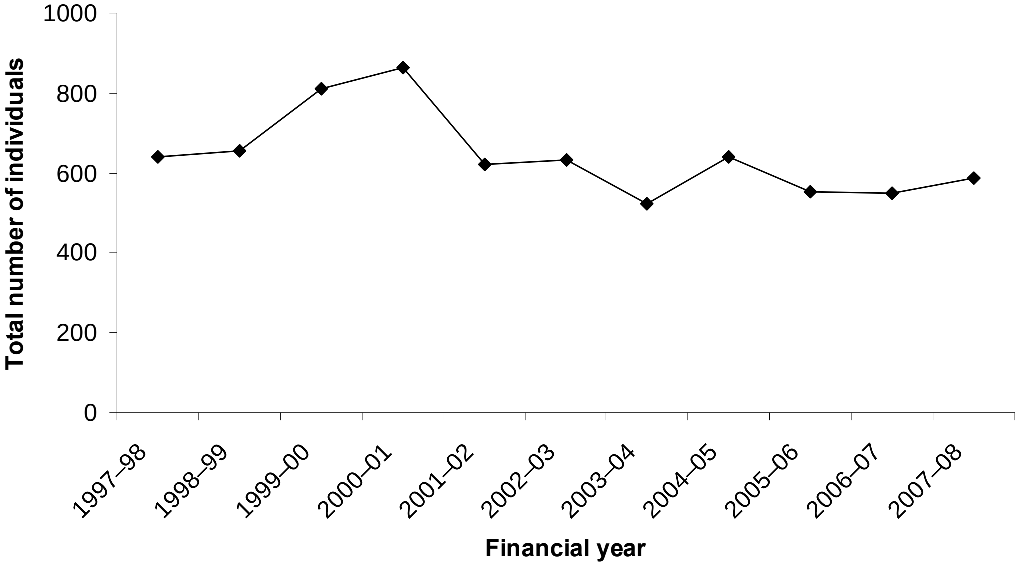


Figure 12. Annual total of sharks caught in Queensland's shark control program between 1997 and 2008. The annual catch is recorded by financial year, rather than calendar year.

Tuna and billfish

Most of the tuna and billfish catch inside the GBRMP comes from the charter line fishery that operates offshore. Between 2005 and 2008, the combined reported catch for tunas and billfishes was 88.3 tonnes. The highest proportion of the catch was made up of black marlin, *Makaira indica*, which accounted for almost 70% of the recorded catch (Figure 13). Yellowfin tuna (*Thunnus albacares*), mackerel tuna (*Euthynnus affinis*) and longtail tuna (*T. tonggol*) made up 12.8, 11.1 and 6.8% respectively, and a relatively small catch of Indo-Pacific blue marlin (*M. mazara*) were recorded.

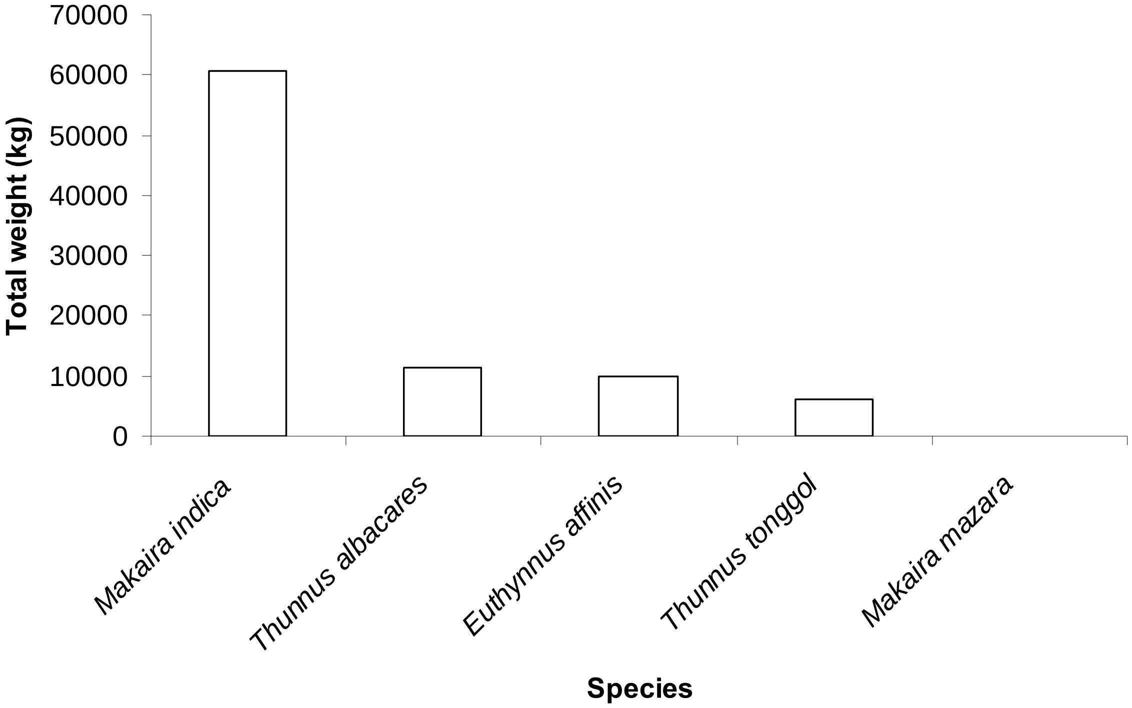


Figure 13. Recorded catch in weight (kg) of tuna and billfish for all commercial and charter fisheries between 2005 and 2008. Data source: QPIF.

Between 2005 and 2008, catch per unit effort (CPUE) remained stable for yellowfin and longtain tuna (*T. albacares* and *T. tonggol*), but underwent some fluctuations for mackerel tuna and black marlin (*E. affinis* and *M. indica*) (Figure 14). Catch rates for *E. affinis* went from approximately 6-7 kg per fishing day to 100 kg per day in 2006, and then returned to the previous lower rates. *M. indica* catch rates declined over the four-year time period, from 60 kg per day to around four.

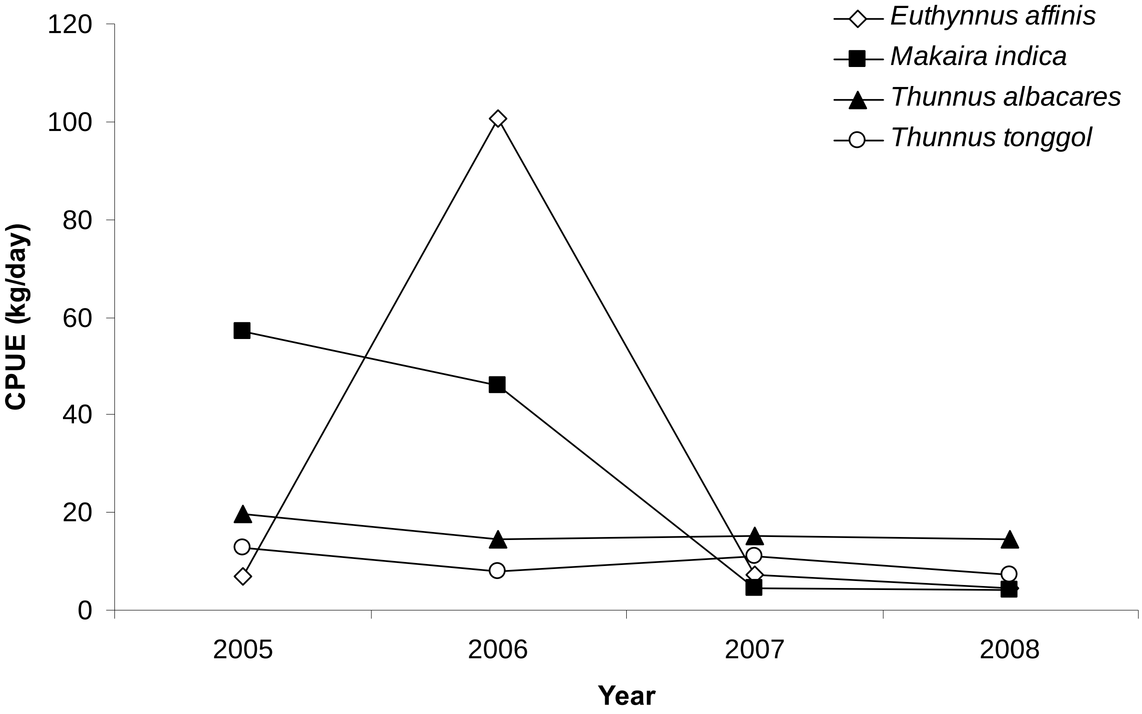


Figure 14. Catch per unit effort (in kg per fishing day) of the four tuna and billfish species most commonly recorded from fisheries inside the GBR. Data source: QPIF.

The ETBF, operating primarily outside the GBRMP, recorded a total catch of 5,217 tonnes in 2007, made up of albacore tuna (53.76%), yellowfin tuna (31.74%), swordfish (15.5%), bigeye tuna (11.27%) and striped marlin (5.12%). Catch rates of billfish are often correlated with lunar phase and the distribution of prey, but most billfish are associated with the upper layers of the water column. The distribution of marlin species also tends to vary seasonally, with southward migrations of black marlin occurring down the east Australian coastline (Lowry et al. 2007). Most tuna species are primarily caught in longline fisheries operating outside the GBRMP. A 50-fold increase in bigeye tuna catches occurred in the 1990s (Evans et al. 2008). The effects of charter fishing on black marlin spawning aggregations, and the impacts of the ETBF on adjacent pelagic habitats within the GBRMP, are unknown.

Plectropomus *species (Coral trout)*

Coral trout, or species of the genus *Plectropomus*, are the principal target of both commercial and recreational line fishers on the GBR (Davis et al. 2004). Even by Australian standards, where fishing pressure is comparatively low, *P. leopardus* and *P. maculatus* are subject to considerable fishing pressure (Frisch & van Herwerden 2006). Mounting evidence suggests that fishing has significantly decreased the abundance and size of coral trout in some parts of the GBR, particularly those close to human population centres (Evans & Russ 2004). It has been suggested that legally harvestable stock of *P. leopardus* on GBR may have been at or near full exploitation under 1996 levels of effort. Despite this, effort was further increased by 35% in the following years, but did not lead to increased catch by any sector (Mapstone et al. 2008). The TAC is now set at 1996 levels (1350 t of coral trout). Localised depletion of coral trout may increase the likelihood of hybridisation, potentially leading to a reduction in genetic diversity, disruption of local adaptation potential, or even species replacement (Frisch & van Herwerden 2006). Furthermore, it is likely to diminish their functional role as local generalist top predators on coral reefs. Fortunately, *P. leopardus* responds well to fishing closures, though there may be a lag; one study observed no effect after 3 years, but a significant increase in density after 8 years (Nardi et al. 2004).

Epinephelus *Species*

Species of cods and groupers of the genus *Epinephelus* are subject to substantial exploitation for the live fish trade. Many of these species are long-lived (reaching up to 40 years of age), locally uncommon (<1 individual per 1000m^2) and form spawning aggregations to reproduce (Pears et al. 2006; 2007). These spawning aggregations have at times been targeted by fishers, despite widespread evidence that this practice is not sustainable (Sadovy de Mitcheson et al. 2008). Targeting spawning aggregations not only has the potential to depress the reproductive success of the populations, it has been calculated that 1,000kg of fish caught from an aggregation can deplete a much greater area than the same biomass caught from non-aggregation populations (Pears et al. 2007). On the GBR, *Epinephelus* species are caught in both the commercial and recreational line fisheries.

Mackerel

The most prominent pelagic species in inshore fisheries is the Spanish mackerel *Scomberomorus commerson*. Fishing gear selectivity can have a large impact on the element of the population removed; while commercial fishing gears select for larger, faster growing mackerel, recreational gears tend to harvest smaller and younger mackerel (Ballagh et al. 2006). Catches of Spanish mackerel in the 2007-2008 financial year were approximately 647 tonnes (DPI&F 2008a).

Spatial Considerations

Spatial information on the locations of catches from the GBR were obtained from QPIF for a number of predator species. The data are summarised for the years from 2005 to 2008. The lack of data from map grids with less than five records of fishing boats means that the total catch estimates are likely to underrepresent the actual catch for each species. These data were overlayed on known distributions of each species on the GBR.

The combined distribution of whaler sharks (Family Charcharhinidae) extends across the GBR shelf and beyond, but catches are concentrated in inshore areas. Northern regions of the GBR also record few or no shark catches, while central and southern regions have the highest overall catches (Figure 15). The majority of the coral trout (*Plectropomus*) catch is from the southern half of the GBR's mid-shelf reefs; this reflects areas where the common coral trout *P. leopardus* is most abundant. Inshore catches are more likely to contain the bar-cheek coral trout *P. maculatus*. Outer shelf catches may be those capturing the rarest coral trout species, the bluespotted coral trout *P. laevis* and the squaretail coral trout *P. areolatus* (Figure 16). Catch and distribution maps for both mackerel species (Spanish mackerel *Scomberomorus commerson* and grey mackerel *S. semifasciatus*) suggests that these species are only exploited across a portion of their range. Spanish mackerel catches are highest in the central section of the GBR and are concentrated along the edges of the reefs, especially in the southern GBR regions where no catches are recorded inshore. Grey mackerel catches are high off Townsville and off Mackay, and tend to follow the coastline rather than the reefs (Figure 17). These patterns suggest that the highest level of predator exploitation occurs on the central and southern GBR.

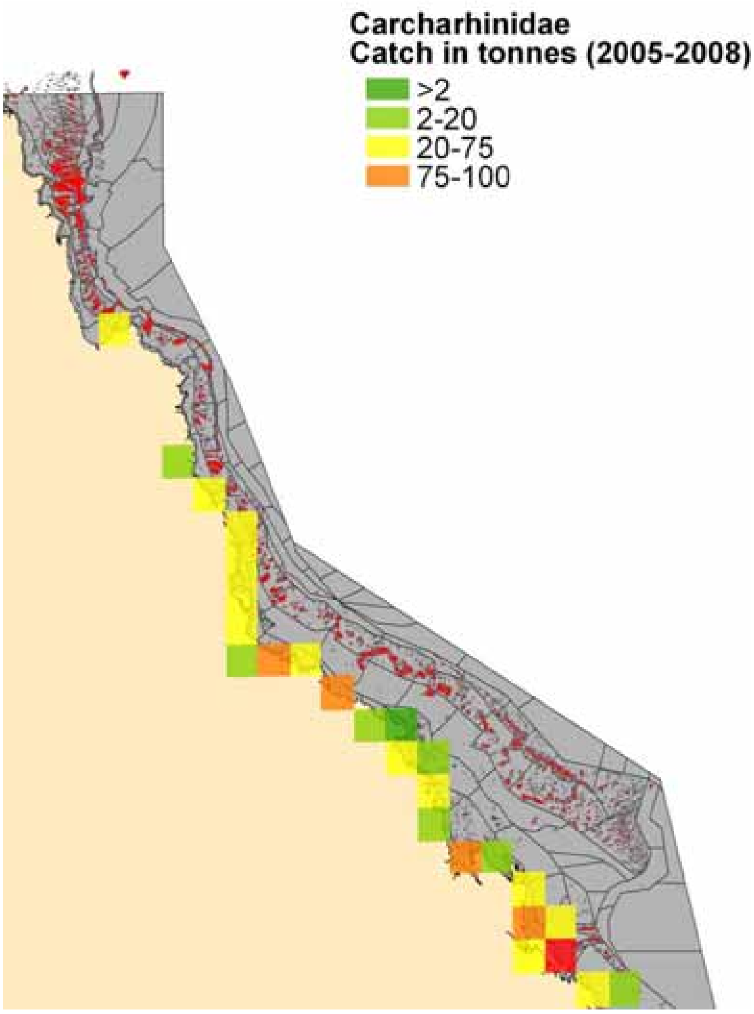


Figure 15. Combined catch 2005-2008 for all carcharhinid (whaler) sharks, overlayed on distribution of sharks across GBR bioregions. Grey: non-reef bioregions; red: reef bioregions. The red grid square represents an outlier of 234 tonnes.

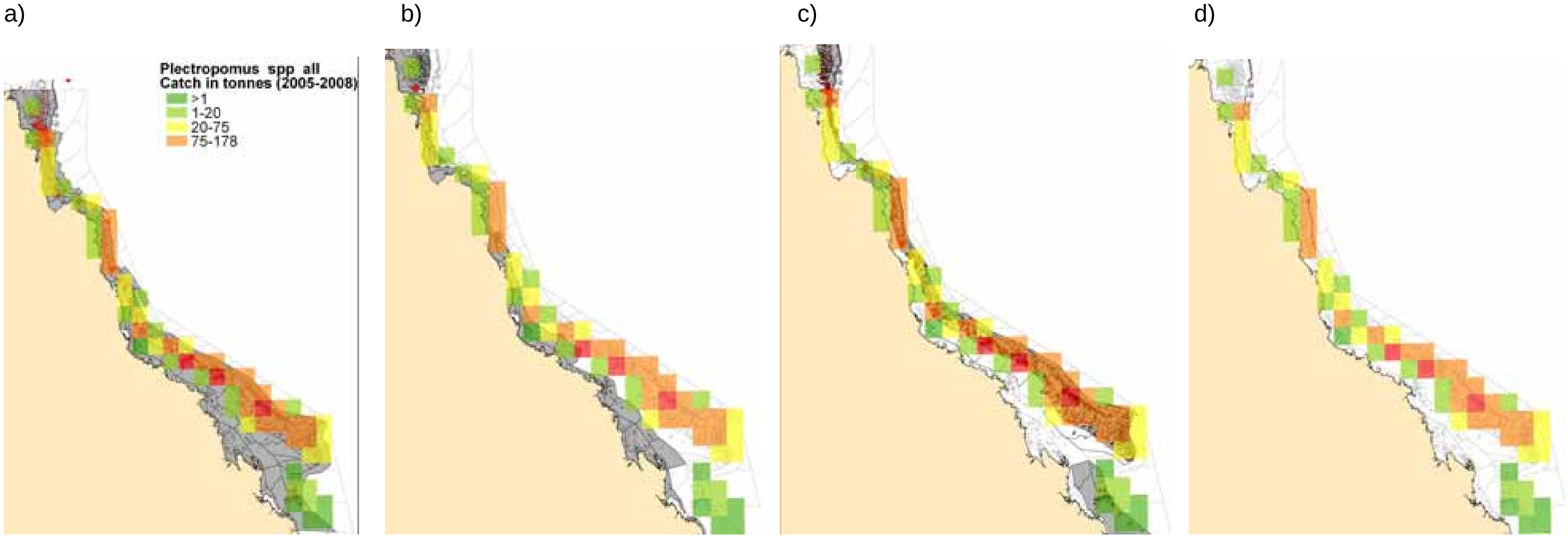


Figure 16. Total catch of all coral trout (*Plectropomus*) species between 2005 and 2008 on the GBR, overlayed on distributions of a) common coral trout, *P. leopardus*; b) bar-cheek coral trout, *P. maculatus*; c) bluespotted coral trout, *P. laevis* and d) squaretail coral trout, *P. areolatus*. Grey: non-reef bioregions; red: reef bioregions. The dark red grid squares represent outliers of greater than 178 tonnes

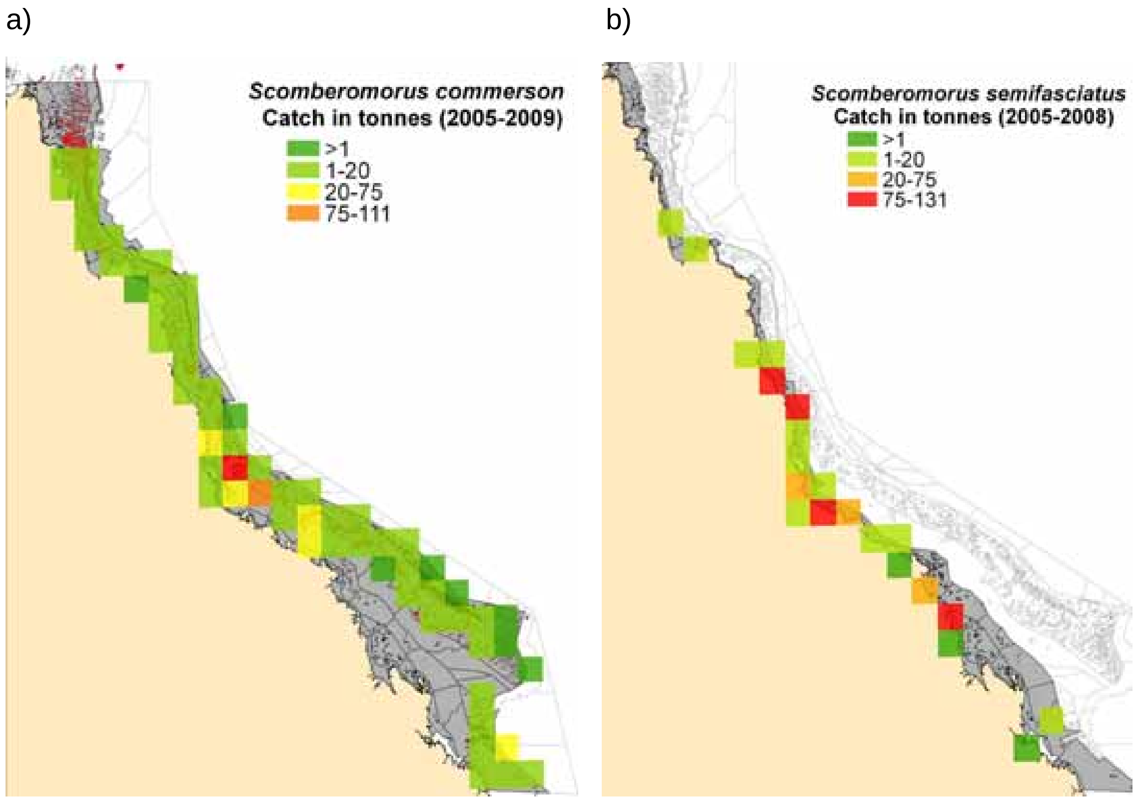


Figure 17. Combined catch 2005-2008 for a) Spanish mackerel *Scomberomorus commerson* (red grid square: 234 t), and b) grey mackerel *S. semifasciatus*, overlayed on distribution of each species across GBR bioregions. Grey: non-reef bioregions; red: reef bioregions.

VULNERABILITY AND RISK ASSESSMENT

Vulnerability Index

Measures of vulnerability used here combine the semi-quantitative method used by Chin and Kyne (2007) to express vulnerability to habitat changes with a measure of intrinsic vulnerability (based on life-history characteristics and susceptibility to overexploitation) which is available on FishBase (Froese & Pauly 2009) for all species of teleosts and elasmobranchs. For reptiles and cetaceans, known life-history parameters were matched with those used to calculate vulnerability in FishBase, to allow the inclusion of these species into the ranking system. The resulting ranking is designed to indicate the relative vulnerability of GBR predators to both habitat degradation (through the ranking of sensitivity and inadaptability) and exploitation (through the ranking of the intrinsic vulnerability).

The most vulnerable of the apex predators are the white shark *Carcharodon carcharias* and the greynurse shark *Carcharias taurus* (Table 8). This is not surprising, given that both these species are protected under federal legislation; their vulnerability is well-recognised and documented, and they are rare in the GBRMP. A variety of uncommon whaler sharks, the two species of mako sharks and the lemon shark are also in the top ten most vulnerable apex predators. Tiger sharks, which are one of the most important GBR predators, have relatively low vulnerability, primarily due to their relatively widespread distribution. Swordfish, scalloped hammerheads, marlin and crocodiles are amongst those to have the lowest vulnerability value; these species are probably those with the highest number of offspring per reproductive event. In general, most apex predators are considered here to be relatively adaptable, primarily due to their high levels of mobility. However, more information is needed on the specific habitat requirements (e.g. for feeding, breeding or nursery grounds) of each species.

Table 8. Vulnerability index (high Index value = high vulnerability) of apex predators.

Species Common	**name**	**Sensitivity**	**Inadaptability**	**Intrinsic Vulnerability**	**Vulnerability index**
Carcharodon carcharias	White shark	1	1	86	86
Carcharias taurus	Greynurse shark	1	0.66	68	44.88
Carcharhinus obscurus	Dusky shark	1	0.33	88	29.04
Sphyrna mokarran	Great hammerhead	1	0.33	85	28.05
Carcharhinus falciformis	Silky shark	1	0.33	79	26.07
Negaprion acutidens	Lemon shark	1	0.33	78	25.74
Isurus paucus	Longfin mako	1	0.33	76	25.08
Carcharhinus longimanus	Oceanic whitetip shark	1	0.33	75	24.75
Carcharhinus albimarginatus	Silvertip shark	1	0.33	74	24.42
Carcharhinus altimus	Bignose shark	1	0.33	74	24.42
Makaira mazara	Indo-Pacific blue marlin	1	0.33	70	23.1

Species	Common name	Sensitivity	Inadaptability	Intrinsic Vulnerability	Vulnerability index
Orcinus orca	Killer whale	1	0.33	65	21.45
Pseudorca crassidens	False killer whale	1	0.33	65	21.45
Isurus oxyrhinchus	Shortfin mako	1	0.33	64	21.12
Carcharhinus leucas	Bull shark	0.66	0.33	87	18.9486
Tetrapturus audax	Striped marlin	1	0.33	55	18.15
Sphyrna leweni	Scalloped hammerhead	0.66	0.33	82	17.8596
Carcharhinus amboinensis	Pigeye shark	0.66	0.33	72	15.6816
Crocodylus porosus	Estuarine crocodile	1	0.33	45	14.85
Makaira indica	Black marlin	1	0.33	44	14.52
Galeocerdo cuvier	Tiger shark	0.66	0.33	64	13.9392
Xiphias gladius	Broadbill swordfish	0.66	0.33	64	13.9392

A variety of inshore and deep water sharks and large groupers are at the top of the vulnerability list for the generalist top predator group (Table 9). Deepwater sharks are considered vulnerable due to their relative rarity, habitat specificity, and life history characteristics, which are often K-selected in deep water organisms (Smith et al. 1998). Inshore sharks, the largest *Epinephelus* species and some of the predatory marine mammals, are in the next most vulnerable category. Many of these species are also relatively rare and slow growing. The least vulnerable species are those with less K-selected life histories and especially those with more adaptable and offshore habitat requirements.

Table 9. Vulnerability index (high Index value = high vulnerability) of generalist top predators.

Species	Common name	Sensitivity	Inadaptability	Intrinsic Vulnerability	Vulnerability index
Hypogaleus hyugaensis	Pencil shark	1	1	62	62.00
Orectolobus maculatus	Spotted wobbegong	1	0.66	85	56.10
Squalus montalbani	Greeneye spurdog	0.66	1	64	42.24
Glyphis glyphis	Speartooth shark	1	0.66	60	39.60
Squalus megalops	Shortnose spurdog	0.66	1	59	38.94
Centrophorus niaukang	Gulper shark	0.66	0.66	87	37.90
Dalatias licha	Kitefin shark	0.66	0.66	81	35.28
Centrophorus moluccensis	Endeavour dogfish	0.66	0.66	69	30.06
Carcharhinus plumbeus	Sandbar shark	1	0.33	86	28.38

Species Common	**name**	**Sensitivity**	**Inadaptability**	**Intrinsic Vulnerability**	**Vulnerability index**
Epinephelus lanceolatus	Queensland groper	1	0.33	85	28.05
Epinephelus malabaricus	Blackspotted rockcod	1	0.33	85	28.05
Ruvettus pretiosus	Oilfish	1	0.33	85	28.05
Echinorhinus cookei	Prickly shark	1	0.33	83	27.39
Epinephelus tukula	Potato rockcod	1	0.33	83	27.39
Triaenodon obesus	Whitetip reef shark	1	0.33	83	27.39
Hexanchus makanurai	Bluntnose sixgill shark	1	0.33	81	26.73
Alopias superciliosus	Bigeye thresher shark	1	0.33	79	26.07
Feresa attenuata	Pygmy killer whale	1	0.33	75	24.75
Steno brendanensis	Rough-toothed dolphins	1	0.33	75	24.75
Istiophorus platypterus	Indo-Pacific sailfish	1	0.33	74	24.42
Gymnosarda unicolor	Dogtooth tuna	1	0.33	73	24.09
Hemipristis elongata	Fossil shark	1	0.33	73	24.09
Carcharhinus limbatus	Common blacktip shark	0.66	0.66	55	23.96
Thunnus alalunga	Albacore	1	0.33	72	23.76
Plectropomus laevis	Bluespotted coral trout	1	0.33	71	23.43
Mesoplodon pacificus	Longman's beaked whale	1	0.33	70	23.10
Orcaella heinsohni	Australian snubfin dolphin	1	0.33	70	23.10
Globicephala macrorhynchus	Short-finned pilot whale	1	0.33	67	22.11
Globicephala melas	Long-finned pilot whale	1	0.33	67	22.11
Delphinus delphis	Short-beaked common dolphin	1	0.33	65	21.45
Carcharhinus melanopterus	Blacktip reef shark	1	0.33	64	21.12
Gempylus serpens	Snake mackerel	1	0.33	63	20.79
Carcharhinus amblyrhynchoides	Graceful shark	1	0.33	60	19.80
Carcharhinus cautus	Nervous shark	1	0.33	58	19.14
Epinephelus coioides	Goldspotted rockcod	1	0.33	58	19.14

Species Common	name	Sensitivity	Inadaptability	Intrinsic Vulnerability	Vulnerability index
Plectropomus areolatus	Passionfruit coral trout	1	0.33	56	18.48
Carcharhinus fitzroyensis	Creek whaler	1	0.33	55	18.15
Sphyraena barracuda	Great barracuda	0.66	0.33	79	17.21
Thunnus tonggol	Longtail tuna	1	0.33	51	16.83
Thunnus albacares	Yellowfin tuna	1	0.33	50	16.50
Sousa chinensis	Indo-Pacific humpbacked dolphin	0.66	0.33	75	16.34
Stenella longirostris	Spinner dolphin	0.66	0.33	75	16.34
Tursiops truncatus aduncus	Bottlenose dolphin	0.66	0.33	75	16.34
Heptranchias perlo	Sharpnose sevengill shark	0.66	0.33	73	15.90
Thunnus obesus	Bigeye tuna	0.66	0.33	72	15.68
Carcharhinus tilstoni	Australian blacktip shark	0.66	0.33	70	15.25
Acanthocybium solandri	Wahoo	1	0.33	46	15.18
Plectropomus leopardus	Common coral trout	1	0.33	46	15.18
Plectropomus maculatus	Barcheek coral trout	1	0.33	46	15.18
Scomberomorus commersoni	Spanish mackerel	1	0.33	46	15.18
Carcharhinus macloti	Hardnose shark	1	0.33	45	14.85
Epinephelus polyphekadion	Camouflage grouper	0.66	0.33	67	14.59
Prionace glauca	Blue shark	0.66	0.33	67	14.59
Tetrapturus angustirostris	Shortbill spearfish	1	0.33	43	14.19
Carcharhinus brevipinna	Spinner shark	0.66	0.33	64	13.94
Eusphyra blochii	Winghead shark	0.66	0.33	60	13.07
Carcharhinus amblyrhinchos	Grey reef shark	0.66	0.33	50	10.89
Epinephelus fuscoguttatus	Flowery rockcod	0.66	0.33	50	10.89
Rhizoprionodon acutus	Milk shark	0.66	0.33	47	10.24
Carcharhinus dussumieri	Whitecheek shark	0.66	0.33	46	10.02
Carcharhinus sorrah	Spot-tail shark	0.66	0.33	46	10.02
Rhizoprionodon taylori	Australian sharpnose	0.66	0.33	41	8.93

Species Common	name	Sensitivity	Inadaptability	Intrinsic Vulnerability	Vulnerability index
	shark				
Sphyraena qenie	Blackfin barracuda	0.33	0.33	77	8.39
Sphyraena jello	Pickhandle barracuda	0.33	0.33	75	8.17
Euthynnus affinis	Mackerel tuna	0.33	0.33	46	5.01
Lutjans bohar	Red bass	0.33	0.33	39	4.25
Scomberomorus semifasciatus	Grey mackerel	0.33	0.33	37	4.03

Species in the high-level mesopredator group are generally less vulnerable than both higher trophic groups, with the exception of the habitat restricted giant moray. The giant moray, rare and deep water sharks, black trevally and humphead Maori wrasse, rank as the most vulnerable high-level mesopredators, reflecting their relative rarity and habitat specificity (Table 10). The Maori wrasse is certainly recognised as being a vulnerable reef fish and is now internationally protected. Lowest vulnerability rankings were found in the smaller snappers, which are generally relatively abundant, as well as dolphinfish, small mackerel and small trevally.

Table 10. Vulnerability index (high Index value = high vulnerability) of high-level mesopredators.

Species Common	name	Sensitivity	Inadaptability	Intrinsic Vulnerability	Vulnerability index
Gymnothorax javanicus	Giant moray eel	1	1	76	76
Hemigaleus australiensis	Australian weasel shark	0.66	1	47	31.02
Cheilinus undulatus	Humpheaded Maori wrasse	1	0.33	73	24.09
Eucrossorhinus dasypogon	Tasselled wobbegong	1	0.33	66	21.78
Caranx lugubris	Black trevally	1	0.33	60	19.8
Lepidocybium flavobrunneum	Escolar	0.66	0.33	85	18.51
Pseudocarcharias kamoharai	Crocodile shark	1	0.33	54	17.82
Orectolobus ornatus	Ornate wobbegong	0.66	0.33	75	16.33
Variola louti	Yellowedge coronation trout	1	0.33	49	16.17
Caranx ignobilis	Giant trevally	0.66	0.33	74	16.12
Epinephelus cyanopodus	Purple rockcod	0.66	0.33	70	15.25
Symphorus nematophorus	Chinamanfish	1	0.33	44	14.52
Caranx papuensis	Brassy trevally	1	0.33	42	13.86
Lutjanus rivulatus	Maori snapper	1	0.33	42	13.86
Aprion virescens	Green jobfish	0.66	0.33	61	13.28

Species Common	name	Sensitivity	Inadaptability	Intrinsic Vulnerability	Vulnerability index
Lutjanus argentimaculatus	Mangrove jack	0.66	0.33	59	12.85
Carangoides orthogrammus	Island trevally	1	0.33	38	12.54
Lutjanus malabaricus	Malabar snapper	0.66	0.33	50	10.89
Caranx melampygus	Bluefin trevally	0.66	0.33	48	10.45
Katsuwonus pelamis	Skipjack tuna	0.66	0.33	46	10.02
Lutjanus monostigma	Onespot snapper	0.66	0.33	40	8.71
Coryphaena hippurus	Common dolphinfish	0.66	0.33	39	8.49
Carangoides fulvoguttatus	Turrum	0.33	0.33	68	7.40
Lethrinus miniatus	Redthroat emperor	0.33	0.33	60	6.53
Scomberomorus queenslandicus	School mackerel	0.33	0.33	45	4.90
Lutjanus gibbus	Paddletail	0.33	0.33	32	3.48

Risk Assessment

The risk assessment was conducted by converting the traditional matrix format into a simple calculation to combine importance (as a proxy for ‘Consequence’) and vulnerability (as a proxy for ‘Likelihood). The resulting risk ratings are designed to assist in the prioritisation of predator species for future research and protection measures.

The highest risk (rating of 5,000+), in terms of the likelihood of losing species from the GBR and the consequences of losing those species based on their relative importance index, is limited to two large and common species of shark (

Table 11): the tiger shark *Galeocerdo cuvier* and the bull shark *Carcharhinus leucas*. The tiger shark is identified as being the most widespread and important apex predator of the GBR, and is regularly caught by fisheries and in shark control bouys. Similarly, the bull shark is widely distributed in the GBR region, ranks as the second most important apex predator, and is frequently caught in inshore netting and shark control programs. The next risk level down (ratings between 1,000 and 5,000) is characterised by other large abundant sharks and the two most abundant large billfish species. The white shark is considered at high risk not so much because of its importance to the overall GBR ecosystem, but due to its very high degree of vulnerability, as recognized by its protected status in Australian waters. Similar factors to those noted above probably contributed to the assessment of a high risk rating for the two hammerhead sharks, while the relatively high rating for crocodiles and dusky sharks relates to their vulnerability. Large and rare cetaceans, billfish and sharks that are of low importance on the GBR, and which also have relatively low vulnerability, scored lowest in the apex predator risk assessment.

Table 11. Risk assessment, multiplying importance and vulnerability indices, for each species of apex predator. Risk levels are: Extreme (>5,000), Very high (1,000-5,000), High (500-999), Moderate (250-499), Low (100-249) and Negligible (<100).

Species Common	**name**	**Importance index**	**Vulnerability index**	**Risk**
Galeocerdo cuvier	Tiger shark	1296	13.9392	18065.2
Carcharhinus leucas	Bull shark	477.4737	18.9486	9047.45
Sphyrna leweni	Scalloped hammerhead	232.1053	17.8596	4145.30
Xiphias gladius	Broadbill swordfish	275.8737	13.9392	3845.45
Sphyrna mokarran	Great hammerhead	110.9558	28.05	3112.31
Carcharodon carcharias	White shark	13.64211	86	1173.22
Tetrapturus audax	Striped marlin	63.66316	18.15	1155.48
Carcharhinus amboinensis	Pigeye shark	53.05263	15.6816	831.95
Crocodylus porosus	Estuarine crocodile	40.92632	14.85	607.75
Negaprion acutidens	Lemon shark	23.49474	25.74	604.75
Carcharhinus obscurus	Dusky shark	16.59789	29.04	482.00
Orcinus orca	Killer whale	18.18947	21.45	390.16
Carcharhinus albimarginatus	Silvertip shark	15.91579	24.42	388.66
Isurus oxyrhinchus	Shortfin mako	18.18947	21.12	384.16
Carcharhinus falciformis	Silky shark	13.64211	26.07	355.64
Carcharias taurus	Greynurse shark	6.063158	44.88	272.11
Isurus paucus	Longfin mako	9.776842	25.08	245.20
Pseudorca crassidens	False killer whale	11.36842	21.45	243.85
Carcharhinus longimanus	Oceanic whitetip shark	9.094737	24.75	225.09
Makaira mazara	Indo-Pacific blue marlin	9.473684	23.1	218.84
Carcharhinus altimus	Bignose shark	5.684211	24.42	138.80
Makaira indica	Black marlin	8.810526	14.52	127.92

A wide range of generalist top predators considered to be at extreme or very high risk in terms of the consequences of their loss from the GBR ecosystem. These include the whitetip and blacktip reef sharks, the deepwater squalid shark *Squalus montalbani* and the K-selected common blacktip shark *Carcharhinus limbatus* (Gunn et al. 2008)(

Table 12). Other species in the ten high risk generalist top predators include three more deepwater sharks, the grey reef shark and the blue shark as well as the yellowfin and albacore tuna. These are all species that are either important, usually in terms of abundance, or have vulnerable life history features. The most at risk reef teleost is the large bluespot coral trout, followed by the very abundant common coral trout; both these species are very important for coral reef habitats and their loss would have dramatic consequences for the ecosystem. Lowest risks are for small pelagic species and the rarer reef predators. The relatively low risk ranking of *Rhizoprionodon taylori* coincides with a low risk ranking for these species in a previous shark fishery risk assessment (Gribble et al. 2005).

Table 12. Risk assessment, multiplying importance and vulnerability indices, for each species of generalist top predator. Extreme (>5,000), Very high (1,000-5,000), High (500-999), Moderate (250-499), Low (100-249) and Negligible (<100).

Species Common	name	Importance index	Vulnerability index	Risk
Triaenodon obesus	Whitetip reef shark	226.7582	27.39	6210.90
Dalatias licha	Black shark	145.7722	35.2836	5143.36
Centrophorus niaukang	Taiwan gulper shark	128.1514	37.8972	4856.57
Carcharhinus limbatus	Common blacktip shark	193.7799	23.958	4642.57
Thunnus alalunga	Albacore	153.1012	23.76	3637.68
Thunnus albacares	Yellowfin tuna	213.8714	16.5	3528.87
Squalus montalbani	Philippine spurdog	76.08988	42.24	3214.03
Carcharhinus melanopterus	Blacktip reef shark	151.9842	21.12	3209.90
Stenella longirostris	Spinner dolphin	188.2223	16.335	3074.61
Carcharhinus tilstoni	Australian blacktip shark	178.5991	15.246	2722.92
Thunnus obesus	Bigeye tuna	173.2313	15.6816	2716.54
Prionace glauca	Blue shark	167.1646	14.5926	2439.36
Centrophorus moluccensis	Endeavour dogfish	80.09461	30.0564	2407.35
Hemipristis elongata	Fossil shark	96.11965	24.09	2315.52
Plectropomus laevis	Bluespotted coral trout	97.34051	23.43	2280.68
Sphyraena barracuda	Great barracuda	131.2385	17.2062	2258.11
Plectropomus leopardus	Common coral trout	144.0138	15.18	2186.13
Carcharhinus amblyrhinchos	Grey reef shark	194.8853	10.89	2122.30
Carcharhinus brevipinna	Spinner shark	150.6767	13.9392	2100.31
Delphinus delphis	Short-beaked common dolphin	96.95547	21.45	2079.69
Alopias superciliosus	Bigeye thresher shark	78.89508	26.07	2056.79
Hexanchus makanurai	Bigeye sixgill shark	75.22407	26.73	2010.73
Hypogaleus hyugaensis	Pencil shark	31.84486	62	1974.38
Squalus megalops	Piked spurdog	50.4176	38.94	1963.26
Glyphis glyphis	Speartooth shark	48.50107	39.6	1920.64
Carcharhinus plumbeus	Sandbar shark	64.06032	28.38	1818.03
Heptranchias perlo	Sharpnose sevengill shark	112.1325	15.8994	1782.83
Echinorhinus cookei	Prickly shark	64.6681	27.39	1771.25
Sousa chinensis	Indo-Pacific humpbacked dolphin	106.3144	16.335	1736.64
Mesoplodon pacificus	Longman's beaked whale	72.75161	23.1	1680.56
Orcaella heinsohni	Australian snubfin dolphin	68.9554	23.1	1592.87
Globicephala melas	Long-finned pilot whale	69.84155	22.11	1544.19
Tursiops truncatus aduncus	Bottlenose dolphin	91.27566	16.335	1490.98
Carcharhinus sorrah	Spot-tail shark	138.5851	10.0188	1388.45
Scomberomorus commersoni	Spanish mackerel	87.14223	15.18	1322.81

Species Common	**name**	**Importance index**	**Vulnerability index**	**Risk**
Acanthocybium solandri	Wahoo	83.5823	15.18	1268.77
Globicephala macrorhynchus	Short-finned pilot whale	57.13426	22.11	1263.23
Epinephelus lanceolatus	Queensland groper	43.65097	28.05	1224.41
Carcharhinus cautus	Nervous shark	62.68673	19.14	1199.82
Istiophorus platypterus	Sailfish	45.26767	24.42	1105.43
Steno brendanensis	Rough-toothed dolphins	42.84261	24.75	1060.35
Tetrapturus angustirostris	Shortbill spearfish	74.36831	14.19	1055.28
Eusphyra blochii	Winghead shark	79.24794	13.068	1035.61
Sphyraena qenie	Blackfin barracuda	119.3639	8.3853	1000.90
Orectolobus maculatus	Spotted wobbegong	16.49036	56.1	925.10
Sphyraena jello	Pickhandle barracuda	105.3211	8.1675	860.21
Feresa attenuata	Pygmy killer whale	33.46574	24.75	828.27
Plectropomus maculatus	Barcheek coral trout	53.59118	15.18	813.51
Carcharhinus fitzroyensis	Creek whaler	43.65097	18.15	792.26
Gymnosarda unicolor	Dogtooth tuna	32.07538	24.09	772.69
Euthynnus affinis	Mackerel tuna	132.3112	5.0094	662.79
Ruvettus pretiosus	Oilfish	23.28052	28.05	653.01
Rhizoprionodon acutus	Milk shark	62.48942	10.2366	639.67
Epinephelus malabaricus	Blackspotted rockcod	22.6985	28.05	636.69
Epinephelus fuscoguttatus	Flowery rockcod	55.34812	10.89	602.74
Gempylus serpens	Snake mackerel	25.86724	20.79	537.77
Epinephelus tukula	Potato rockcod	19.40043	27.39	531.37
Carcharhinus amblyrhynchoides	Graceful shark	25.86724	19.8	512.17
Carcharhinus dussumieri	Whitecheek shark	46.58302	10.0188	466.70
Carcharhinus macloti	Hardnose shark	28.41798	14.85	422.00
Epinephelus coioides	Goldspotted rockcod	18.44937	19.14	353.12
Lutjans bohar	Red bass	81.10366	4.2471	344.45
Rhizoprionodon taylori	Australian sharpnose shark	36.21413	8.9298	323.38
Thunnus tonggol	Longtail tuna	18.75375	16.83	315.62
Scomberomorus semifasciatus	Grey mackerel	77.5033	4.0293	312.28
Plectropomus areolatus	Passionfruit coral trout	16.8924	18.48	312.17
Epinephelus polyphekadion	Camouflage grouper	16.07392	14.5926	234.56

All the risk ratings of about half of the high-level mesopredators rate as ‘low’ to ‘negligible’ under the combined risk assessment. This is to be expected given their lower trophic standing in GBR marine communities (Table 13). Apart from the giant moray, the species in need of potential prioritisation are the deepwater escolar, the giant trevally, the humphead Maori wrasse (which is already protected) and the common dolphinfish. The smaller lutjanids and trevallies and the redthroat emperor are generally rated at lower risk than the other predators in this list: they are usually less abundant and have a higher population turnover rate than their larger relatives (Marriott et al. 2007).

Table 13. Risk assessment, multiplying importance and vulnerability indices, for each species of high-level mesopredators. Risk levels are: Extreme (>5,000), Very high (1,000-5,000), High (500-999), Moderate (250-499), Low (100-249) and Negligible (<100).

Species Common	**name**	**Importance index**	**Vulnerability index**	**Risk**
Gymnothorax javanicus	Giant moray	90.60452	76	6885.94
Caranx ignobilis	Giant trevally	155.9006	16.1172	2512.68
Lepidocybium flavobrunneum	Escolar	113.6171	18.513	2103.39
Cheilinus undulatus	Humphead Maori wrasse	49.81687	24.09	1200.08
Coryphaena hippurus	Mahi mahi	119.298	8.4942	1013.34
Caranx melampygus	Bluefin trevally	71.95255	10.4544	752.22
Epinephelus cyanopodus	Purple rockcod	44.31859	15.246	675.68
Carangoides fulvoguttatus	Turrum	89.06021	7.4052	659.50
Lutjanus malabaricus	Saddletail snapper	55.02374	10.89	599.20
Katsuwonus pelamis	Skipjack tuna	56.90793	10.0188	570.14
Symphorus nematophorus	Chinamanfish	38.35295	14.52	556.88
Variola louti	Yellowedge coronation trout	34.20082	16.17	553.02
Lutjanus argentimaculatus	Mangrove jack	42.60642	12.8502	547.50
Eucrossorhinus dasypogon	Tasselled wobbegong	20.89558	21.78	455.10
Aprion virescens	Green jobfish	31.8128	13.2858	422.65
Orectolobus ornatus	Ornate wobbegong	24.60863	16.335	401.98
Scomberomorus queenslandicus	School mackerel	74.21684	4.9005	363.69
Hemigaleus australiensis	Australian weasel shark	10.67024	31.02	330.99
Pseudocarcharias kamoharai	Crocodile shark	14.22698	17.82	253.52
Caranx lugubris	Black trevally	9.700215	19.8	192.06
Lethrinus miniatus	Redthroat emperor	27.85442	6.534	182.00
Carangoides orthogrammus	Thicklip trevally	12.53735	12.54	157.21
Lutjanus monostigma	Onespot snapper	10.39388	8.712	90.55
Lutjanus rivulatus	Maori snapper	6.081801	13.86	84.29
Caranx papuensis	Brassy trevally	5.690793	13.86	78.87
Lutjanus gibbus	Paddletail	15.53518	3.4848	54.13

COMBINED EFFECTS OF CLIMATE CHANGE AND PREDATOR EXPLOITATION

The pressure from human activities such as fishing may increase vulnerability of apex predators to climate change (Chin & Kyne 2007). The most common management recommendation in the face of climate change predictions has been to protect ecosystems from other more localised pressures, such as fishing and pollution. Well managed fisheries, for instance, are expected to enhance the recovery potential of coral reefs after coral mortality (Cinner et al. 2009). However, both the role and status of many predators and the predictions of future climate change effects are subject to high levels of uncertainty. This must be taken into account when assessing the possible consequences of climate change in an ecosystem from which large predators have been depleted.

Current levels of coral degradation resulting from storms, bleaching events and water quality decline are already having measurable effects on reef fish communities. This is especially true for species that depend on living corals for food, shelter and recruitment (Wilson et al. 2006; Cinner et al. 2009). While this does not usually include species of high-level predators, it does have implications for the future availability of prey (Graham et al. 2007). Management of the GBR and elsewhere is now focusing less on fisheries management and more on maintaining biodiversity, ecosystem processes and resilience. Managing for resilience requires acknowledging the need to sustain the reef's functional groups and ecological processes. Intact functional groups are thought to underpin the resilience of coral reefs to disturbance, and understanding their roles is a crucial step towards directing management and monitoring efforts (Bellwood et al. 2004). Over the last five decades, reefs in the Indo-Pacific (Bruno & Selig 2007) and on the GBR have shown system wide decline in coral cover and increased numbers of reefs damaged by either *Acanthaster planci* starfish outbreaks, coral bleaching, or both (Bellwood et al. 2004). The potential for a diversity of responses to a changing climate greatly enhances reef resilience. It is important to place knowledge on the current exploitation levels of apex predators in the context of concurrent declines in the quality of the habitat that sustains them.

Current Knowledge: Climate Change and Predators

Coral bleaching and declining water quality are currently considered to be two of the most important large-scale factors affecting the Great Barrier Reef (Hoegh-Guldberg et al. 2007; Cooper et al. 2009). Changing climate and weather patterns have already resulted in significant damage to many habitats of the GBR (Fabricius et al. 2005), and have affected even offshore pelagic systems and seabird breeding success (Congdon et al. 2008). A recent review of information on the effects of climate change on the GBR's sharks and rays indicated that according to current knowledge, ten climate change drivers, including changes in ocean temperature, pH, salinity and other physical characteristics are likely to affect chondrichthyan communities (Chin & Kyne 2007). This could be extrapolated to include all predators. The effects of current environmental conditions on apex predators are poorly understood and have been only sporadically documented, but GBR ecosystems are expected to suffer the impacts of predicted changes in environmental conditions, including temperature and UV radiation, ocean acidity and salinity, sea level changes, storm and flood frequency and ocean circulation.

Changes in water temperature may affect predator populations through habitat degradation and, at the level of the individual, through physiological changes.

Metabolic rates in ectotherms are intimately linked to their surrounding temperatures, and increasing temperatures generally cause metabolic rates to increase (Chin & Kyne 2007). Behaviour and seasonal density variations can also be temperature-dependent, including the large-scale patterns of habitat use by large sharks (Wirsing et al. 2007b). The most resilient species are likely to be those that are already exposed to a range of temperatures, such as inshore and estuarine predators, and those that are able to move across large-scale habitats (Tullis & Baillie 2005). At the same time, however, future temperature fluctuations may be greater in nearshore environments (Chin & Kyne 2007), placing inshore species under additional stress. Changes in water temperature may lead to changes in species' geographic range or habitat preferences. On the GBR, this could result in the loss of rare species that already occur primarily at the edges of the GBRMP. Warmer waters could also facilitate the spread of parasites and diseases (Lafferty et al. 2004).

There is also the concern that during El Niño events that lead to increased sea surface temperature (SST), reductions in cloud cover and wave action can lead to greater penetration of ultraviolet (UV) radiation through the water column. Changes in levels of UV can alter nutrient cycling and productivity by affecting the microbial communities in the water column; this can lead to changes in the location or strength of localised upwellings and areas of high productivity on the GBR (Kingsford & Welch 2007). Large schools of prey are generally attracted by upwellings and targeted by large predators; changes in the availability of these aggregations of prey can be detrimental. Habitats critical to apex predator breeding, nursery grounds and feeding areas may also be damaged by increased UV radiation (Sheaves et al. 2007).

There is much uncertainty around the predictions for changes in pH and salinity, and the effects that these changes will have on apex predators is unknown. However the acid/base (pH) balance in sharks and rays is tightly regulated, and they can compensate for acidity changes by rapid pH buffering (Chin & Kyne 2007). Increased frequency and intensity of storms and droughts is forecast to bring greater variability in the amount of freshwater entering the GBR lagoon (Meynecke et al. 2006). The increased variability in rainfall will also result in greater salinity extremes. This is likely to affect the habitats of the inshore GBR, and in some cases freshwater flooding has caused widespread bleaching due to salinity decreases. This can affect predators that rely on nearshore habitats as nurseries or feeding areas (Chin & Kyne 2007).

The East Australian Current (EAC) is the main current affecting the GBR as it passes through the GBR lagoon, and the reefs and island chains create localised eddies (Kingsford & Wolanski 2008). Many large-bodied and highly mobile species rely on these currents and eddies to facilitate long-range movements (Kingsford & Welch 2007). There is concern that changes in climate could cause the bifurcation point of the EAC to move south, and that increased current strength may lower thermoclines and reduce the strength of upwelling currents (Kingsford & Welch 2007). This can result in changes in prey availability, migration patterns and the timing of baitfish aggregations or plankton blooms (Chin & Kyne 2007). El Niño Southern Oscillation (ENSO) and upwellings have been linked to significant changes in prey availability that caused collapses in fisheries and seabird populations (Kingsford & Welch 2007; Congdon et al. 2008).

Future Climate Change Scenario

In the last 100 years, atmospheric concentrations of CO_2 have risen from approximately 300 parts per million (ppm) to 380ppm, average SST has increased by 0.74°C, sea level has risen by 17cm, carbonate concentrations have declined by approximately 30mmol kg^{-1} seawater and pH has decreased by 0.1pH unit towards higher acidity (IPCC 2007), although the natural variability of the pH in waters of the GBR is still unknown. In the next 100 years, the Intergovernmental Panel for Climate Change (IPCC) predicts an increase in SST of between 1 and 3°C, sea level rise of 0.1-0.9m and declines in ocean pH of between 0.4 and 0.5 (IPCC 2007). The effects of these changes on marine tropical ecosystems are currently subject to much experimental research and predictive modelling, and are expected to be largely detrimental (Meynecke et al. 2006; Hoegh-Guldberg et al. 2007). Studies have shown that the resilience of ecosystems to these predicted changes will depend on a number of key ecosystem-specific components, such as the maintenance of herbivore densities on coral reefs, to prevent macroalgal overgrowth during expected higher levels of coral mortality (Hughes et al. 2007). Given current levels of predator exploitation, what are the likely effects of depleted predator communities on the GBR under the climate change scenario predicted by the IPCC?

Given the lack of consensus and paucity of evidence for the role of high-level predators as a functional group, predictions of likely impacts of climate change on ecosystems with depleted predator populations are largely speculative. Indeed, many believe that large predators have already largely disappeared from marine habitats around the world (Jackson et al. 2001; Myers & Worm 2003). Further research is required into how predators affect ecosystems, both healthy and degraded (Heithaus et al. 2008a); the following discussion is designed to stimulate the formulation of potential research directions. Previous analysis of rapid warming in the ocean showed an oscillation between top-down and bottom-up control of ecosystems (Litzow & Ciannelli 2007); the shift from top-down to bottom-up control is the most likely consequence of a combination of potentially disruptive environmental changes and the depletion of top predators. The synergy between predator decline and the overall ecosystem effects of global climate change are likely to differ between the main ecosystems of the GBR.

Coral Reefs

Predicted rapid increases in SST and ocean acidity are expected to affect coral reefs through widespread coral mortality and overgrowth of reefs by fleshy macroalgae (Hughes et al. 2003; Hoegh-Guldberg et al. 2007; De'ath et al. 2009). Healthy populations of herbivores are expected to prevent the shift in dominance from corals to algae, and herbivore exploitation on the GBR is negligible (Hughes et al. 2007; Frisch et al. 2008). However, where there are added stresses such as overfishing, pollution and nutrient enrichment (e.g. on inshore coral reefs), the recovery of live coral cover may be impaired. Mortality of reef-building corals, and the consequent erosion of the overall reef structure, may affect the quality of habitat for reef fish (Graham et al. 2006). The most directly affected species are those that depend on living coral for food and/or shelter, which may in turn affect prey availability for coral reef predators (Graham et al. 2008).

On coral reefs where predators have been depleted, the ability of the ecosystem to recover from disturbance may be altered. While direct evidence is very scarce, a small number of studies suggest that predators are an important contributor to overall reef biodiversity, and through this, to reef resilience. For instance, protected coral reefs with larger populations of predators also host greatly reduced densities of the corallivorous starfish, *Acanthaster planci* (Sweatman 2008). The correlation between higher predator density and reduced coral mortality from starfish predation suggests one way in which predators increase the potential resilience of coral communities. DeMartini et al. (2008) suggest that there is a positive relationship between the biomass of large predators and the cover of live coral. Other workers suggest that protecting predators through fishing closures automatically enhances biodiversity, and that this is what promotes greater resilience (Jones et al. 2007). The relevance of these claims for the GBR needs to be investigated.

The diets of common coral reef predators, coral trout of the genus *Plectropomus*, include the juvenile stages of herbivorous parrotfish (Graham et al. 2003). If predators consume herbivores that are needed to reduce macroalgal biomass, areas with greater predator biomass could be perceived as being more at risk from algal overgrowth (Mumby et al. 2006). However, empirical evidence of this does not exist, and at least one study has shown that numbers of large herbivores are enhanced in areas where predators are also protected (Nardi et al. 2004), and Caribbean studies indicated that large parrotfish escape predation pressure in proected areas, and therefore effectively reduce macroalgae and enhance coral recruitment (Mumby et al. 2006; Mumby et al. 2007). Any relationship between predators and coral reef health in the face of climate change predictions can only be inferred from isolated studies; even so it is only relevant to generalist top predators. Effects of depleted apex predator numbers on the GBR's coral reefs are unknown.

Inshore and inter-reef

Inshore and inter-reef habitats are predicted to be subject to similar temperature fluctuations as coral reefs, and can be more or less vulnerable depending on the composition of the benthic community. For example, seagrass meadows may be more severely affected than sparsely colonised soft-sediment habitat. Inshore habitats are also likely to be subject to localised and pulsed fluctuations in salinity, turbidity and water quality (Hutchings et al. 2007). Australia's key climate change predictions include an increase in overall dryness, as well as increased storm intensity and frequency, which can cause greater salinity fluctuations in coastal areas (Meynecke et al. 2006). Inshore habitats are also likely to have predator communities that have already been heavily depleted, due to their greater accessibility to fishers and their proximity to land-based anthropogenic habitat destruction.

Reduced predator densities in inshore and inter-reef habitats may change the diversity and community composition of prey. Where these ecosystems are relatively simple, trophic cascades may be hastened by changed environmental conditions (Pinnegar et al. 2000). Phase shifts in simple ecosystems are more likely to occur under combined conditions of changed top-down (ie. predatory) and bottom-up (ie. nutrient availability, physical conditions) processes (Litzow & Ciannelli 2007). This may also affect inshore fisheries catches. It is well-known that estuarine and inshore catches fluctuate with changing rainfall (Meynecke et al. 2006). The effects of the predicted increases in rainfall fluctuations on both predators and their catchability for fisheries are unknown.

Concurrent changes in predator densities and habitat condition or availability may change patterns of habitat use by megafauna such as turtles, dugongs and dolphins. Current research shows megafauna in Shark Bay distinctly responds to the risk of tiger shark predation, which is expected to have flow-on effects on seagrasses and prey (Heithaus et al. 2009). How the effects of climate change might influence these patterns in conditions of reduced predator densities is unknown.

Pelagic and deep water

While the open ocean and pelagic ecosystems may be somewhat more buffered against rapid temperature, salinity and pH changes, climate change may also affect currents and upwellings (Kingsford & Welch 2007) through the potential changes in interactions of key Pacific and Indian Ocean climate patterns (Behera et al. 2006). This may affect the spatial availability of nutrients and prey, and may disrupt migration routes and spawning aggregations. Many of the large-scale patterns in fish community composition on the GBR are driven by the position of the EAC's bifurcation point (Cappo et al. 2007); changes in the location of this major current system may affect the spatial patterns in species distributions.

Pelagic ecosystems are relatively simple when compared with complex benthic habitats such as coral reefs, and trophic cascades may be more likely here when large predators are depleted (Myers et al. 2007). However, pelagic habitats are key in the connectivity between benthic habitats, and pelagic predators can represent key linkages between inshore, offshore and benthic habitats through seasonal or ontogenetic movements (Kingsford & Welch 2007). The highly dynamic nature of the pelagic environment, combined with the general lack of information on these ecosystems, makes it impossible to predict the consequences of predator depletion in the context of climate change predictions.

DISCUSSION AND CONCLUSIONS

This review has identified 115 species of top-level predators for the GBR, including 22 apex predators, 67 generalist top predators and 26 high-level mesopredators. The 22 species of apex predators, the most important of which have been identified as the tiger shark and the bull shark, are the largest, most wide-ranging consumers of other large marine animals in the region. The generalist top predators are composed of sharks, teleosts and cetaceans that have more easily defined home ranges and prey on a variety of large and small piscivores. The high-level mesopredators are made up of important, site-attached predatory fish that consume significant portions of fish and invertebrates. Many of the predator species across the three categories are exploited and declining in abundance on the GBR. Recent research indicates a link between declines in predator numbers and ecosystem changes, disruptions in the balance of lower trophic levels, changes in prey community composition and increased vulnerability of reefs to pests, diseases and climate change. Despite high levels of uncertainty surrounding these relationships, the GBR offers a unique opportunity for both legislative protection of species groups, and for a targeted research program to resolve the uncertainty surrounding the effects of removing predators from its ecosystems.

Role and importance of predation

Predation is important in structuring prey communities, but its effect on ecosystems depends on the specific characteristics of the fish communities and their habitats (Heithaus et al. 2008a). The role of predators is clearer in simpler ecosystems, where empirical evidence and theoretical models show that the removal of top consumers is likely to result in large-scale ecosystem changes (Stevens et al. 2000). On the GBR, the removal of predators through human exploitation is likely to affect the population and community dynamics of other reef organisms (DeMartini et al. 2008). While the extent and nature of these changes are not well understood, changes in the abundance of lower trophic levels, and therefore overall community composition, are likely to have destabilising effects on the ecosystem (Myers et al. 2007). On the GBR, direct evidence of such community changes includes altered abundances of prey species (Graham et al. 2003) and the reduction of the corallivorous starfish *Acanthaster planci* and lower incidences of coral disease in Green Zones, where predators are protected (Sweatman 2008; Raymundo et al. 2009).

According to a semi-quantitative ranking of importance, the most important apex predator on the GBR is the tiger shark. This large shark is among the top consumers in all habitats of the GBR; its importance ranking therefore reflects well on what is currently known about this species. Rankings of importance, vulnerability and risk for many of the other species here must be viewed as relative, due to the lack of accurate knowledge of their overall abundance, importance and role on the GBR. Furthermore, much of the information used to calculate the importance indices must be refined once more knowledge is gained of species abundances, distributions and diets. The role of organisms such as cetaceans and crocodiles, which visit the GBRMP on a transient basis, is unknown.

Generalist top predators and high-level mesopredators are of greater local importance than highly transient apex predators. Relatively site-attached sharks, such as the three species of reef sharks, and large cods and groupers are some of the most important generalist top predators on coral reefs, while tunas and billfish perform an important role in the pelagic system, and sharks that are specialised to utilise inshore habitats are likely to affect those areas to a greater degree. The relative importance of the three predator categories is likely to depend on their relative abundance within each ecosystem. For example, coral reefs host only relatively few apex predators and it is likely that the generalist top predators are more important in coral reef communities. High-level mesopredators were included in this study due to the frequent reference to these species as 'top' or 'apex' predators in the literature, and their importance as predators of key invertebrate groups. Most of the current knowledge about the role of predation comes from studies on these generalist top predators and high-level mesopredators.

Vulnerability of top predators

Some predator populations on the GBR are in decline. Many species are preferentially targeted by fisheries, on the GBR and elsewhere. Even species considered relatively productive, such as coral trout, are exploited to a point of reduced densities and sizes in zones open to fishing (Williamson et al. 2004). The difficulty in adequately monitoring large pelagic animals makes it harder to set sustainable limits for harvesting. The most recent global estimate for all recorded shark species is that they declined by 50% in the 8 to 15 years prior to 2003 (Baum et al. 2003).

There is currently widespread concern about the sustainability of exploiting sharks, both worldwide and on the GBR (DEH 2005). Cartilaginous fishes are at greater risk of extinction than bony fishes (Stevens et al. 2000; Myers & Worm 2003), and shark fisheries are generally plagued by a poor sustainability record (Stevens et al. 2000). While some scientists argue that sharks can be harvested sustainably, they admit that this is true only for a small number of relatively productive species (Walker 1998). Estimates of the total global catch from all sources have ranged as high as 100 million sharks annually (Griffin et al. 2008). Shark populations in the GBR region may also be in decline, with dramatically increasing commercial and recreational catch rates between 1994 and 2003 (Henry & Lyle 2003; Gribble et al. 2005). In other areas, such as the Mediterranean, large predatory sharks are considered functionally extinct (Ferretti et al. 2008). Lack of baseline data on shark populations makes it difficult to measure the extent to which they have been depleted, but studies comparing areas open and closed to fishing confirm that declines in numbers of several shark species are occurring on the GBR (Ley et al. 2002; Robbins et al. 2006; Ayling & Choat 2008; Cappo et al. 2009; Heupel et al. 2009b).

Unfortunately, fisheries that take sharks on the GBR are multi-species fisheries directed at more productive and more highly valued teleost species, making it difficult to manage the sustainability of the shark catch alone. This is true of the ECIFF, where sharks are a poorly identified portion of the overall catch. In this fishery, catches of Australian blacktip shark (*Carcharhinus tilstoni*) are not differentiated from the much less productive common blacktip (*C. limbatus*), as these two species are difficult to distinguish (Gunn et al. 2008). Further research is required to verify the status of shark populations on the GBR and to assess what level of harvest, if any, can be sustained without endangering those populations (Heupel et al. 2009b). Despite the lack of information, commercial catches of inshore sharks nearly quadrupled on the GBR between 1994 and 2003 (Gribble et al. 2005). Robbins et al. (2006) estimated that reductions in annual fishing mortality of 36% for whitetip reef shark and 49% for grey reef shark are necessary for population stability. Calculating the annual mortality required for population stability would provide a useful initial tool for the assessment of sustainability for all harvested shark species.

Protection and management

Marine Park zoning has been found to be effective in protecting shark populations from fishing; there were significantly more sharks in no-take Green Zones (Heupel et al. 2009b), and even greater numbers in no-go Pink Zones (Robbins et al. 2006; Ayling & Choat 2008). The success of Pink Zones in protecting shark populations is hampered by their rarity; they make up only 1% of the area of the GBRMP. Furthermore, there is evidence to suggest that areas closed to extractive activities generally support higher overall biodiversity. However, Green Zones are likely to be successful in protecting stock only of species that are relatively site-attached, and that are unlikely to often travel across Green Zone boundaries. Species of apex predators identified in this report, especially those at high risk, may require legislative protection.

There is a great deal of uncertainty about the combined effects of future environmental conditions that are predicted under climate change and the depletion of large predators. Predicted changes in temperature, weather patterns and ocean chemistry are expected to destabilise ecosystems; resilient ones that have effective protection are expected to bounce back and more or less maintain their character (Hughes et al. 2003). There is evidence to suggest that more diverse and complex systems are more resilient, because of functional redundancy, where multiple species are able to perform a similar role and therefore the loss of individual species has smaller repercussions. However, safeguarding resilience requires maintaining trophic structure, and this will require the precautionary safeguarding of all species in the system (Duffy 2002). Research in other areas suggests that predators are the keystone functional group in the maintenance of trophic structure (Myers et al. 2007), community composition (Baum & Worm 2009) and ecosystem complexity (Raymundo et al. 2009). This information from other systems, and recent GBR research linking higher predator numbers to declining COTs outbreaks (Sweatman 2008) and lower incidences of coral disease (Raymundo et al. 2009), suggests that top predators play a key role in maintaining resilience (Sandin et al. 2008).

Conclusions

The top predator functional group of the GBR is comprised of three categories: apex predators (22 species), generalist top predators (67 species) and high-level mesopredators (26 species). Most of these species face some degree of exploitation in the GBRMP. Targeted research can help establish their role with more certainty through detailed comparisons of fished and unfished zones. Management and conservation of GBR top predators will require both legislative protection and targeted research programs to clarify the ecosystem effects of predator depletion. This understanding must be developed specifically for GBR ecosystems, where the role of predators may differ from other areas where research has taken place. In the meantime, the precautionary principle dictates that the protection of top predators is important to avoid greater losses from this functional group before its role and importance is more clearly understood.

Historical accounts suggest that before the advent of industrialised fishing, large predators were 10-20 times more abundant in the oceans than they are today (Myers & Worm 2003; Baum & Worm 2009). The lack of data from before fishing began makes it difficult to determine whether current populations of large predators are still performing their functional roles (Jackson et al. 2001). Recent research has shown that areas protected from fishing, either by remoteness or legislation, host greater numbers of large predators than fished areas. The depletion of apex predators has been found to release mesopredators from predation pressure, causing their numbers to increase and exerting pressure on lower trophic levels (Myers et al. 2007). The presence of healthy predator populations from all three functional groups is expected to prevent the dominance of space and energy by a few competitively superior species and, by thus promoting biodiversity, to enhance resilience (McCann 2007).

Predictions of likely impacts of climate change on ecosystems with depleted predator populations are by necessity largely speculative, but the link between predators and accepted ecological signals of resilience suggest that they play an important role. Recent studies indicate that higher predator numbers are associated with lower incidence of coral disease (Raymundo et al. 2009) and detrimental outbreaks of corallivorous starfish (Sweatman 2008). The ability to withstand the predicted pressures of climate change will be more likely in an ecosystem with greater complexity and lower pre-existing stressors (Bellwood et al. 2004; Birkeland 2004). While the exact mechanisms are still unclear, emerging science suggests a strong link between higher predator numbers and more resilient ecosystems (Sandin et al. 2008).

Predators are the most important group of marine organisms for fisheries around the world. Without protection or truly sustainable harvest strategies, this resource will become functionally extinct or disappear altogether. On the GBR, the most important economic activities – tourism and fisheries – rely to a large extent on the continued presence of healthy populations of predators. The lack of clear evidence of their ecosystem role is of concern, and should not be taken to imply a lack of importance. Research designed to answer questions raised about the effects on prey and overall ecosystems is urgently required. Furthermore, it is necessary to value predators in their own right, rather than just for their anthropogenic value. Until these research needs are fulfilled, the precautionary principle should prevail.

Recommendations

Protection and management

- Improved integration is required between fisheries and ecosystem management and a better application of ecosystem-based fisheries management (Pikitch et al. 2004). For instance, a panel charged with reviewing the proposed new management arrangements for the ECIFF considered that more stringent measures could be put in place to account for the fact that this fishery is operating within a MPA in a World Heritage Area, and that arrangements to protect the sustainability of sharks were not sufficient. However, the new management arrangements included scope for a shark TAC of 600t, and for interactions with protected species (Gunn et al. 2008).
- It is recommended that the GBRMPA assess the viability of establishing a greater number and area of Pink (no-go) Zones on the GBR; recent work on a number of generalist top predators suggests a much better level of compliance in Pink Zones than Green (no-take) Zones. It is recommended that the GBRMPA investigate the viability, cost and logistics of enabling further legislative protection of predators, prioritising species for consideration according to this review's risk assessment.
- Improved education is required on the importance of green zone compliance. Better enforcement and stricter penalties for infringing on green zones; current levels are not adequately deterring non-compliant fishers (Ayling & Choat 2008).

Research

The principal question concerning the role and importance of top predators on the GBR that remains unanswered is: "What will happen to the rest of the ecosystem if the top predators are, or have already been, removed?" The GBR offers a unique system in which to design a research program that seeks to answer this question. It is large, encompasses a variety of different habitats, exhibits a number of environmental and anthropogenic impact gradients and is subject to an existing zoning system that has resulted in areas that harbour predator communities at different densities. Specifically, long-term monitoring of no-go Pink Zones embedded within large no-take Green Zones may provide the best tool for understanding ecosystems where predator densities are most likely to be at 'natural' levels. A better understanding of the role of predators on the GBR requires research on the predators themselves, and also more ecosystem-level research.

- Effective censuses of the status and catch of those species prioritised through the risk assessment (especially those falling into the 'extreme' and 'very high' risk categories are an essential first step towards understanding the current status of the most important predators on the GBR. This would help to determine which species are undergoing the greatest decline, and assist in further prioritising limited resources for more detailed biological and ecological studies.
- Distribution, abundance and life-history data is required for many of the predator species. Some of this research is underway for some species, but it needs to be completed for all exploited GBR sharks as a priority. It is suggested that research on individual species be prioritised according to this review's importance index and / or risk assessment. Research on individual species, particularly sharks, should include:

  - Life history and habitat use information for all species, especially those caught by fisheries and prioritising the most ‘at risk’;
  - Logbooks and observer programs that distinguish between species as much as possible. Better effort and catch data for all species across all fisheries, with better and more regular reporting mechanisms;
  - Records of how many sharks a year are taken as by-catch;
  - Determine overall GBR exploitation rates of ‘at risk’ species including all fisheries and sectors, and deaths from other factors;
  - Better understanding of post-release survival rates from all sectors, including charter;
  - Develop a list of potential no-take species based on the least productive sharks caught by all fisheries. This will help identify where there is not enough knowledge to make a species ‘no-take’ and direct research on particular species.
- It is recommended that a targeted research program be developed to specifically undertake ecosystem-level comparisons between different zones, including reef and non-reef habitats. Factors to consider for such a research program include:
  - Making use of large-scale latitudinal gradients and cross-shelf gradients in anthropogenic pressure;
  - Incorporating gradients in fishing pressure within areas open to fishing;
  - Incorporating zoning-related gradients in fishing pressure (long-term monitoring of no-go Pink Zones embedded within large no-take Green Zones may provide the best tool for understanding ecosystems where predator densities are most likely to be at ‘natural’ levels);
  - Considering all the GBR’s major habitat types: coral reefs, inshore and inter-reef areas, pelagic and deep-water environments. Research has begun to target non-coral reef areas and a future program on the role of predators on the GBR will benefit from incorporating the expertise of researchers that are already examining these systems.
  - Using current accepted sampling designs that allow sufficient replication at all levels, and that take into account sampling techniques relevant to the species and to the habitat (e.g. visual surveys are useful in clear water, while tagging studies and catch data may be more efficient in inshore turbid waters and remote techniques are suitable for deep water);
  - Selecting a wide range of ecosystem response variables, including potential prey species, competitors, key functional groups such as herbivores, invertebrate feeders and macro-invertebrates, habitat structure and complexity, and the community composition of benthic organisms.

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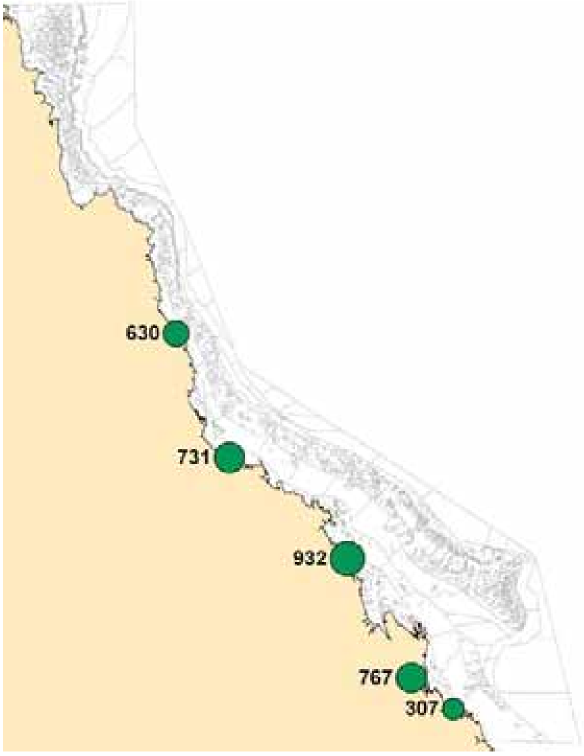
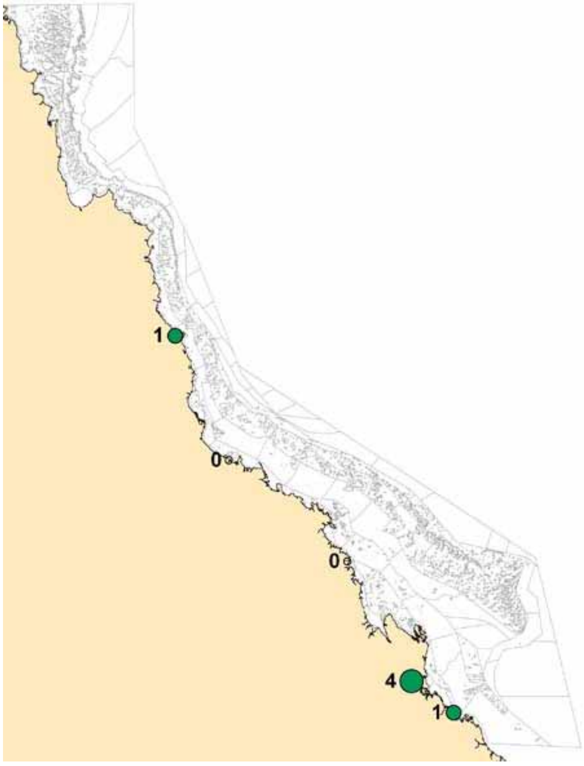
APPENDIX 1 – MAPS OF APEX PREDATORS IN SHARK CONTROL CATCH RECORDS 1996-2006

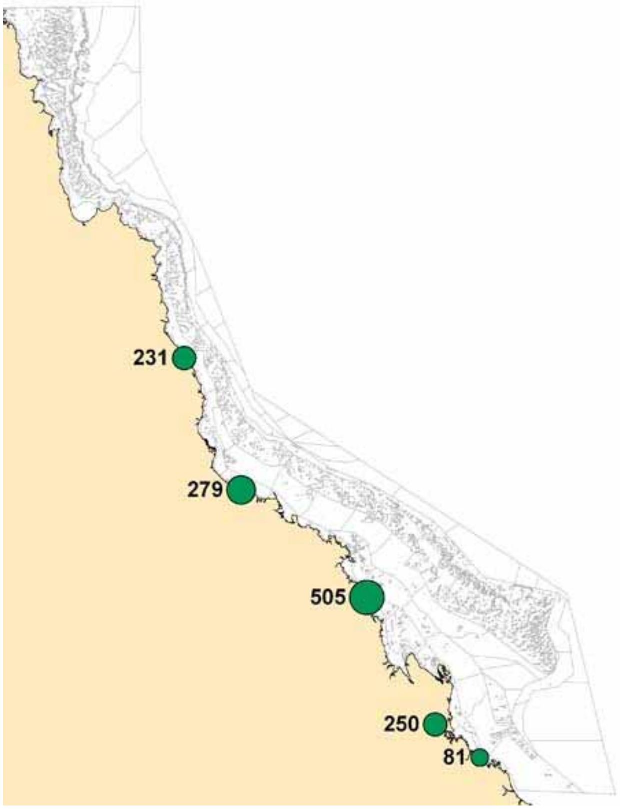
All sharks



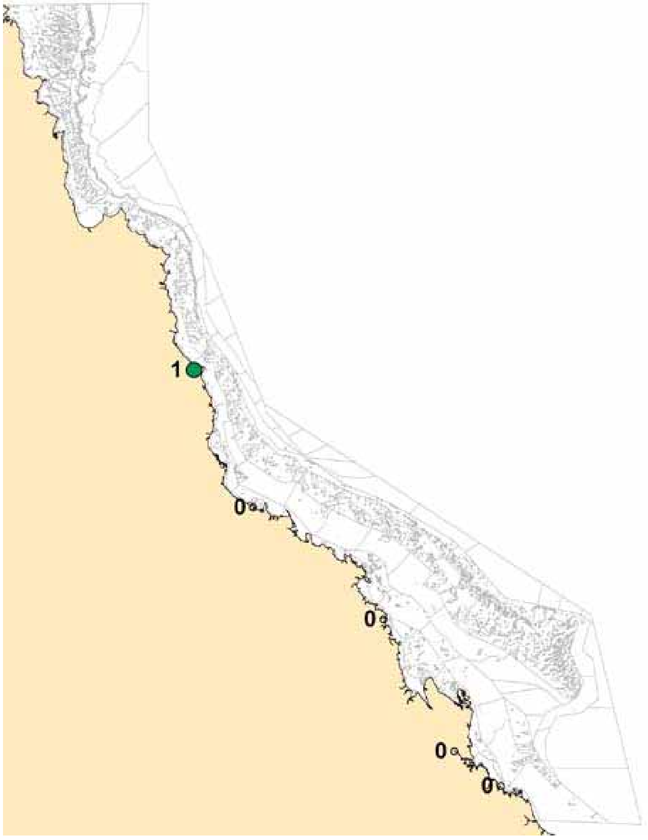
Great white shark, *Carcharodon carcharias*



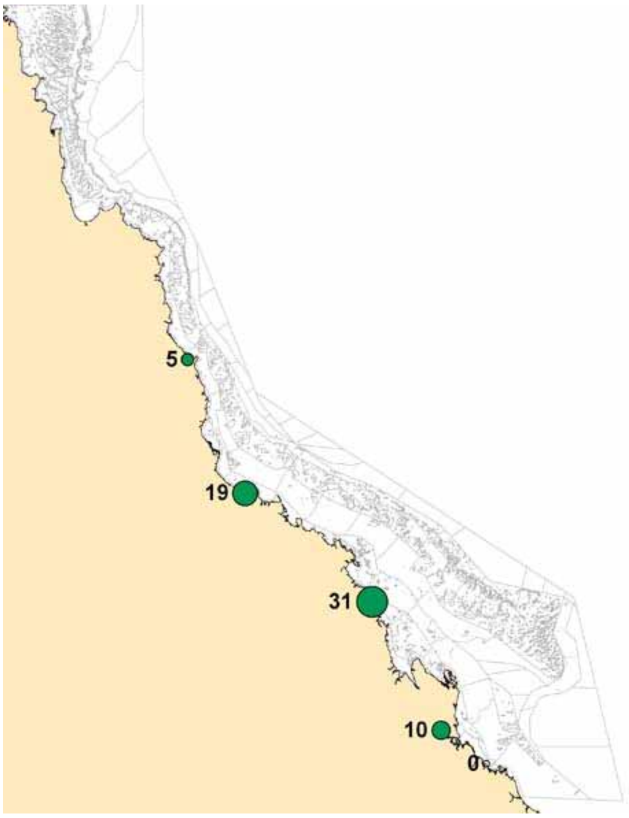
Tiger shark, *Galeocerdo cuvier*



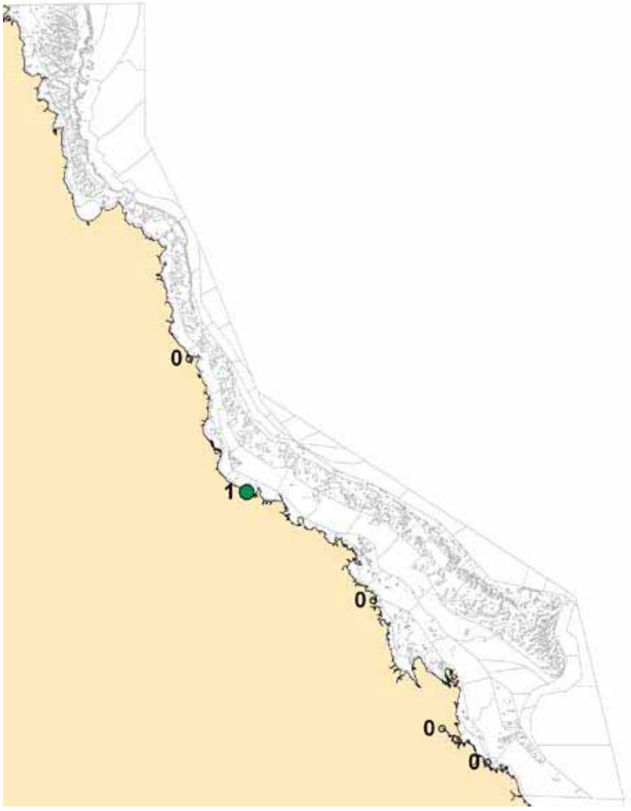
Silky shark, *Carcharhinus falciformis*



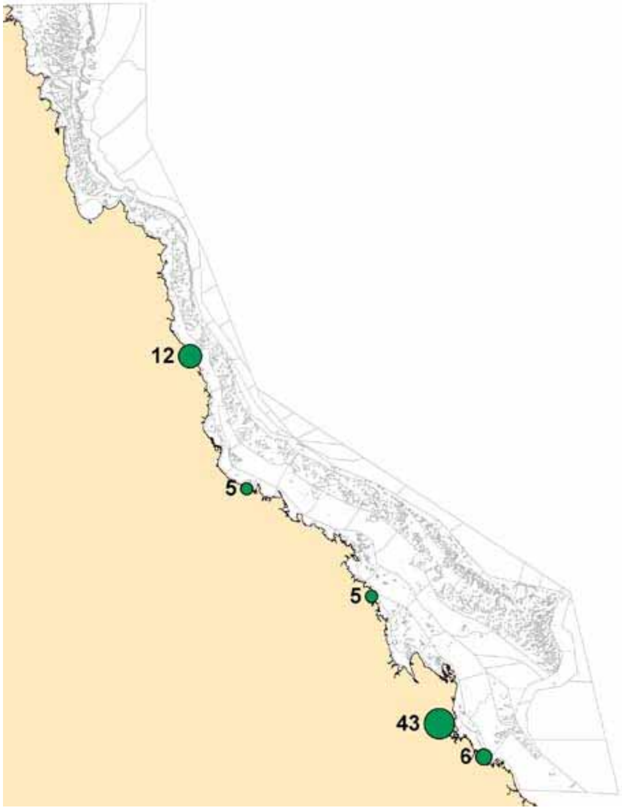
Pigeye shark, Carcharhinus amboinensis



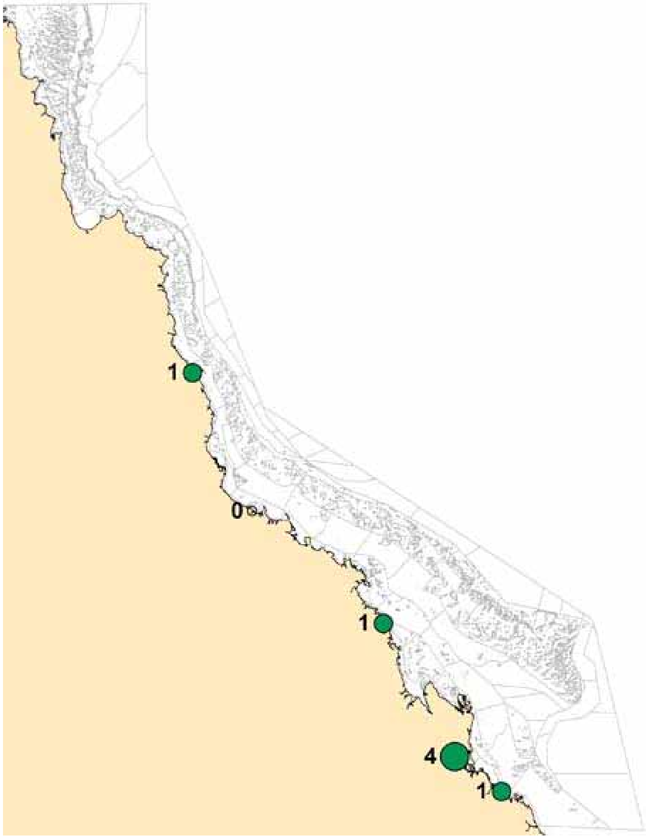
Mako shark, *Isurus* sp.



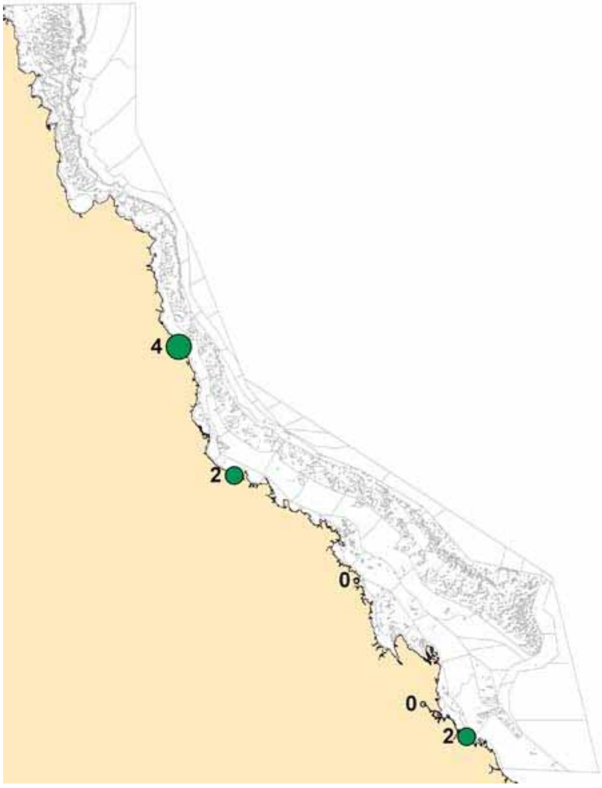
Hammerhead sharks, *Sphyrna* spp.



Greynurse shark, *Carcharias taurus*



Dusky shark, *Carcharhinus obscurus*



Bull shark, *Carcharhinus leucas*