

**Aspects of the biology of elasmobranchs in a subtropical embayment in
Western Australia and of chondrichthyan fisheries in Indonesia**

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DECLARATION

**I declare that the information contained in this
thesis is the result of my own research
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Abstract

The first aim of this thesis was to test the hypothesis that the spatial and food resources in the nearshore waters of a subtropical embayment in Western Australia (Shark Bay) will be partitioned within and amongst the main elasmobranch species that occur in that large water body. The size and age compositions, growth rates and reproductive biology of females and males of the nervous shark *Carcharhinus cautus* in Shark Bay were then determined to better understand the mode of life of this abundant species in this embayment. The second aim was to determine the species and size compositions of chondrichthyans landed by fisheries employing different methods in south-eastern Indonesia. The implications of these data for management were next determined and aspects of the reproductive biology of the most abundant of those species were explored, in a very preliminary manner.

The nearshore, shallow waters of Shark Bay are used as a nursery area by several shark species and the different habitats in those waters are partitioned, to a certain degree, amongst those species. Ten species of shark (5 families), five species of ray (4 families) and twelve species of teleost (10 families) were caught in those waters. *Carcharhinus cautus* was the most abundant species, contributing 59.9% to the total number of elasmobranchs and 42.3% to all fish caught. This species and *Negaprion acutidens* were collected mainly or entirely from unvegetated sites, whereas *Rhizoprionodon acutus*, *Carcharhinus brevipinna* and *Chiloscyllium punctatum* were caught largely or exclusively at the seagrass site. The number of elasmobranch species and number of individuals of elasmobranchs were greatest in the seagrass site and least in the unvegetated site where no vegetation was present nearby, and they were significantly less in the latter site than in the one where dense mangroves were present nearby. These two biotic variables were also

significantly greater in summer and autumn than in winter when temperatures were lowest. The species composition of elasmobranchs in each habitat type almost invariably differed significantly from that in each of the other habitat types and there was evidence that the species composition of elasmobranchs varied in a similar seasonal manner at the three unvegetated sites. *Carcharhinus cautus*, and probably also *Hemigaleus microstoma* and *Chiloscyllium punctatum*, were the only species that completed their life cycles in the nearshore, shallow waters of Herald Bight. However, the capture of the juveniles of a further four species with umbilical scars emphasises the importance of these waters as a nursery habitat for shark species.

The dietary compositions of one ray species (*Rhinobatus typus*) and three shark species (*Carcharhinus cautus*, *Negaprion acutidens*, *Rhizoprionodon acutus*) undergo size-related changes and differ among these species, thereby reducing the potential for competition for food within and among these four species. *Rhinobatus typus* fed almost exclusively on penaeid prawns and portunid crabs, which is reflected in its narrow dietary breadth, whereas different species of teleosts constituted a major component of the diets of each size class of the three shark species. The relative contributions of the different species of teleost to the diets of the three shark species varied. The variations in dietary composition among the four species reflect differences in behaviour, modes of feeding and relative mouth sizes.

Carcharhinus cautus copulates in late October–early November, shortly followed by ovulation (and thus conception) and parturition occurs about 11 months later. The reproductive cycle of *C. cautus* is biennial. Female and male *C. cautus* reached *ca* 28 and 32% of their lengths at their maximum observed ages, respectively, at the time of parturition. Females and males of *C. cautus* attained maximum total lengths of 1330 and 1110 mm, respectively, and maximum ages after parturition of 16 and 12 years,

respectively. Maturity was attained at about 1010 mm by females and 910 mm by males and at least 50% of females and males had become mature by the end of their sixth and fourth years of life, respectively. The three-parameter von Bertalanffy growth curves provided reasonably good fits to the lengths at age of females and males of *C. cautus* during just postnatal life and throughout the whole of pre- and postnatal life. However, the four-parameter Schnute growth curve significantly improved the fit to these data for both females and males from conception and for females from birth. The question of when, from a biological view point, it might be appropriate to switch from using a von Bertalanffy growth curve to the more complex Schnute growth curve are discussed.

A total of 139 chondrichthyan species, comprising 77 species of shark representing 17 families, 61 species of ray representing 11 families and a single species of holocephalan, were recorded at the ten landing sites surveyed in south-eastern Indonesia. However, it should be recognised that up to 49 of the 139 chondrichthyan species recorded have apparently not yet been described and thus assigned a species name. The most speciose and commonly recorded families were the Dasyatidae and Carcharhinidae, which collectively contributed 84.8%, respectively, to the total number of individuals of all species. The use of MDS ordination demonstrated that the species compositions at the eight main landing sites reflected to a greater extent the fishing methods used rather than the geographical location of those sites. Data on the reproductive biology of males demonstrated that a number of elasmobranch species were fished prior to the time that they attained maturity.

The three most abundant chondrichthyan species that were caught both as juveniles and adults were *Dasyatis kuhlii*, *Dasyatis zugei* and *Himantura walga*. Since the reproductive cycle of each of these species did not follow a seasonal pattern, the timing of conception and parturition and the duration of gestation of these species could not be determined. The fecundity of these three species was very low, *i.e.* maximum of two but

usually only a single embryo. The size at maturity of the three species, using data on the prevalence of mature fish, ranged from minima of 163 mm for females and males of *H. walga* to maxima of 237 mm for females and 239 mm for males of *D. kuhlii*. The translucent zones on the vertebral centra of *D. kuhlii* were apparently deposited annually and were thus used to estimate the ages of the individuals of this species. The maximum estimated ages of female and male *D. kuhlii* were 15 and 10 years, respectively.

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Publications

The publications listed below form the basis for chapters 5 and 4, respectively.

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CHAPTER 1

General Introduction

1.1 The class Chondrichthyes

The subclass Elasmobranchii is the major group of the class Chondrichthyes, containing *ca* 96% of the 929–1164 extant chondrichthyan species (Compagno, 1999). The remaining chondrichthyan species belong to the subclass Holocephalii (chimaeras and elephant fishes). The Elasmobranchii can be further divided into the Selachii (sharks) and Batoidea (rays). The Selachii consists of eight major orders, *i.e.* Hexanchiformes (six- and sevengill and frilled sharks), Squaliformes (dogfish sharks), Pristiophoriformes (sawsharks), Squatiniformes (angel sharks), Heterodontiformes (bullhead sharks), Orectolobiformes (carpet sharks), Lamniformes (mackerel sharks) and Carcharhiniformes (ground sharks and requiem sharks) (Compagno, 1999). The Batoidea contains a single order, the Rajiformes, which contains all rays, *i.e.* sawfishes, guitarfishes, shovelnose rays, electric rays, skates, stingrays, stingarees, eagle rays and manta rays (Carpenter & Niem, 1999). The two most speciose and abundant of the elasmobranch families that are found in inshore waters of the subtropical and tropical regions of the world are the Carcharhinidae and Dasyatidae (Last & Stevens, 1994; Carpenter & Niem, 1998, 1999).

1.1.1 Family Carcharhinidae

The Carcharhinidae (whaler or requiem sharks) is one of the largest families of sharks and the most important of those families in terms of artisanal and commercial fisheries in tropical regions (Compagno, 1984; Bonfil, 1994; Castillo-Géniz *et al.*, 1998). The maximum length of members of this family range widely from 0.7 m, as, for example, with the Borneo shark *Carcharhinus borneensis* and the Australian sharpnose shark *Rhizoprionodon taylori*, to 6.0 m for the tiger shark *Galeocerdo cuvier*. There are twelve carcharhinid genera, *i.e.* *Carcharhinus*, *Galeocerdo*, *Glyphis*, *Isogomphodon*, *Lamiopsis*, *Loxodon*, *Nasolamia*, *Negaprion*, *Prionace*, *Rhizoprionodon*, *Scoliodon* and *Triaenodon*, of

which the most speciose by far is *Carcharhinus* (Compagno, 1988). The members of the Carcharhinidae are characterised by their possession of fusiform bodies, five pairs of gill slits, two spineless dorsal fins, an anal fin, a non-lunate caudal fin, precaudal pits on their caudal peduncle and a scroll-type intestinal valve (Last & Stevens, 1994). Although carcharhinids are typically viviparous, *i.e.* possess yolk sac placenta, the tiger shark *Galeocerdo cuvier* is aplacentally viviparous, *i.e.* relies solely on substantial yolk reserves (Last & Stevens, 1994).

The nervous shark *Carcharhinus caudatus*, whose biology is studied in detail during this PhD, is a small carcharhinid that is found in northern Australia, from Carnarvon in Western Australia (*ca* 25°S) to Bundaberg in Queensland (*ca* 25°S), and whose distribution extends into southern Papua New Guinea and the Solomon Islands (Last & Stevens, 1994). This species, which has a length of between 350 and 400 mm at birth and attains a maximum length of approximately 1500 mm, is abundant in inshore waters, especially those of marine embayments and mangrove estuaries (Lyle, 1987). This species is characterised by its possession of a rounded snout, basal cusplets on the upper teeth and black tips on the lower caudal lobe and undersurfaces of the pectoral fins, and by the absence of an interdorsal ridge (Plate 1.1) (Last & Stevens, 1994).

1.1.2 Family *Dasyatidae*

The Dasyatidae (stingrays) is the most speciose and abundant batoid family in inshore tropical waters of the world, where its members make a very important contribution to both the artisanal and commercial fisheries (Carpenter & Niem, 1999). This family is represented by more than 60 living species that each belong to one of five genera, *i.e.* *Dasyatis*, *Himantura*, *Pastinachus*, *Taeniura* and *Urogymnus*, with the majority residing in the first two of these genera (Last & Stevens, 1994). The maximum disc widths

of the members of this family range from 180 mm in the dwarf whipray *Himantura walga* to at least 2100 mm in the smooth stingray *Dasyatis brevicaudata* (Last & Stevens, 1994; Carpenter & Niem, 1999). The members of this family contain a circular or rhomboidal-shaped flattened disc, a head that is not demarcated from the rest of the disc, a tail that is generally longer than the disc and is often whip-like, and they do not possess dorsal, anal and caudal fins (Last & Stevens, 1994). The majority of dasyatids are demersal and live on continental shelves, but one species, *i.e.* the pelagic stingray *Dasyatis violacea*, is pelagic in open oceans. Dasyatids display aplacental viviparity, with the functional uterus containing numerous villi that supply histotroph, *i.e.* uterine “milk”, to the embryos in the later stages of development (Wourms, 1977). Certain aspects of the biology of three small dasyatid species, *i.e.* *Dasyatis kuhlii*, *Dasyatis zugei* and *Himantura walga*, which are caught commercially in south-east Asia, were examined in this thesis.

The bluespotted maskray *Dasyatis kuhlii* is a small dasyatid that is widespread in the tropical Indian and western Pacific Oceans, *i.e.* from southern Africa westwards to Micronesia and from Japan southwards to tropical Australia (Carpenter & Niem, 1999). *Dasyatis kuhlii* has a disc width at birth of about 160 mm and attains a maximum disc width of approximately 380 mm (Last & Stevens, 1994). This species, which is very common in inshore waters in depths of up to about 90 m, occurs predominantly over sandy substrates (Last & Stevens, 1994). It is characterised by a rhomboidal disc, a tail with prominent dorsal and ventral skin folds that is banded black and white behind the sting, a dorsal disc surface with prominent blue spots and a dark transverse band across the eyes (Plates 1.2) (Last & Stevens, 1994).

The sharpnose stingray *Dasyatis zugei* is a small dasyatid that attains a disc width of approximately 290 mm and is found in the Indo-West Pacific from India through to southern Japan (Carpenter & Niem, 1999). This species is characterised by its possession of

a rhomboidal disc, an extremely elongated snout and a tail with a narrow ventral skin fold and with no banding beyond the sting (Plates 1.3) (Carpenter & Niem, 1999). Very little is known about the biology of this species.

The dwarf whipray *Himantura walga*, which is the smallest of the dasyatid species, with a maximum disc width of only 180 mm, has a limited distribution in the Indo-West Pacific from Thailand to south-eastern Indonesia (Carpenter & Niem, 1999). The habitat of *H. walga* is poorly defined, but this species is most common in inshore waters and in large coastal embayments. This species is characterised by an oval disc, a tail that lacks skin folds or banding and tip bulbous beyond sting in adult females, a plain-coloured dorsal surface and an entirely white ventral surface, and elongated thorns on the tail (Plates 1.4) (Carpenter & Niem, 1999).

1.2 Resource partitioning in fish communities

When a number of fish species occur in the same environment, the potential for interspecific competition may be reduced by the partitioning of resources within and among those species along spatial, temporal and/or trophic axes (Helfman, 1978; Schoener, 1983; Ross, 1986). Several studies have explored quantitatively the ways in which the resources in a particular environment are partitioned amongst the various species of teleost fish in that environment (Edgar & Shaw, 1995; Jenkins *et al.*, 1997; Platell & Potter, 2001). For example, in the context of space, the species compositions of fish communities in vegetated areas, *e.g.* seagrass or mangroves, often differ from those in adjacent unvegetated areas, *e.g.* over bare sand, reflecting that certain species tend to occur predominantly or exclusively in one or the other of these two habitat types (*e.g.* Lubbers *et al.*, 1990; Ferrell & Bell, 1991; Dean *et al.*, 2000; Gudetti, 2000). Although, at the trophic level, co-occurring fish species often feed on the same prey types, *e.g.* planktonic prey, they each ingest

different relative amounts of each of the prey and, thus, reduce the likelihood of interspecific competition for the food resources in the local environment (*e.g.* Brewer *et al.*, 1995; Edgar & Shaw, 1995; Linke *et al.*, 2001; Platell & Potter, 2001).

Ross (1986) concluded that, when fish species co-occur in the same area, the resources that are most likely to be partitioned amongst those species are firstly food and then habitat. However, these resources may also be partitioned at a temporal level through, for example, differences in the time of year when either the various species occupy a given habitat or when they feed, *e.g.* night vs day (*e.g.* Piet & Guruge, 1997; Platell & Potter, 1999; Linke *et al.*, 2001). Furthermore, since the types of food ingested by most fish species change with body size (*e.g.* Werner & Gilliam, 1984; Schafer *et al.*, 2002), the extent to which there is likely to be potential for competition for food resources within and amongst species will depend, to a certain extent, on the relative sizes of the individuals of each species and of the different species.

1.3 Distribution by water depth and movements of elasmobranchs

Elasmobranchs inhabit a diverse range of habitats, ranging from freshwater rivers in the Amazon region, 4000 km from the coast, to marine waters in excess of 3000 m in depth (Last & Stevens, 1994). Shallow, intertidal waters in tropical and subtropical regions, such as those found in mangroves in estuaries and over sand flats, are typically inhabited by shovelnose rays, whiplays and smaller requiem sharks. Shallow waters with sandy or seagrass substrata are inhabited by bottom-dwelling species, *e.g.* stingrays, angel sharks, shovelnose rays, and also some cruising sharks that rarely settle on the bottom, *e.g.* tiger, lemon, whaler sharks and eagle and bat rays (Last & Stevens, 1994; Tricas *et al.*, 1997). Shallow reef regions are inhabited by a wide variety of reef-dwelling species that are camouflaged by possessing colouration similar to the substrata, *e.g.* catsharks, wobbegongs,

hornsharks, swell sharks and stingrays, whereas other sharks, *e.g.* whaler sharks, whale sharks and hammerheads, are sometimes abundant adjacent to reefs in deeper waters (Tricas *et al.*, 1997). Continental shelf regions, where depths are less than 30 m, are commonly inhabited by similar groups, *e.g.* stingarees, stingrays and angel sharks.

Continental shelf regions between 30 and 200 m in depth support a variety of demersal and pelagic elasmobranchs. Demersal species include skates, stingarees, dogfishes, and angel and hound sharks (Peres & Vooren, 1991; Last & Stevens, 1994), whereas pelagic species include thresher, blue and mako sharks and manta rays (Hazin *et al.*, 1994; Tricas *et al.*, 1997). Deeper regions of the continental slope, *i.e.* over 200 m, are also inhabited by demersal species, *e.g.* gulper sharks, and both epipelagic, *e.g.* thresher and blue sharks, and mesopelagic species, *e.g.* cookiecutter, crocodile and megamouth sharks (Tricas *et al.*, 1997).

The extents to which sharks and rays move within and between different habitats vary greatly. For example, the blue shark *Prionace glauca* is capable of trans-oceanic migrations in excess of 16,000 km, whereas some species of hornsharks have been observed foraging in the same area of reef each day and returning to shelter in the same cave every night (Tricas *et al.*, 1997). Some species, such as the grey reef shark *Carcharhinus amblyrhynchos*, form small to large aggregations over reefs, whereas the white shark *Carcharodon carcharias* is more nomadic, with no specific home range (Last & Stevens, 1994; Tricas *et al.*, 1997; Economakis & Lobel, 1998). Other elasmobranchs, *e.g.* cownose rays in the North Atlantic Ocean, undergo migrations in response to temperature changes, whereas other species, *e.g.* the whale shark *Rhincodon typus* and the shortfin mako shark *Isurus oxyrinchus*, migrate to areas where there is a greater abundance of food or they follow the migrations of their prey (Smith & Merriner, 1987; Last & Stevens, 1994; Tricas *et al.*, 1997). Segregation by sex is also a common characteristic of

elasmobranchs. For example, the females of the scalloped hammerhead shark *Sphyrna lewini* move offshore at a smaller size than their males and thus form aggregations of medium-sized females (Klimley, 1987).

1.4 Partitioning of food resources among elasmobranchs

Since elasmobranchs are often the most abundant and largest predator within marine environments, especially in the subtropical and tropical regions of the world, analyses of the diets and feeding habits of these large predators facilitate a greater understanding of the trophic dynamics that are occurring in these environments. Skates and urolophids are important predators in those demersal environments in which they are abundant (Holden & Tucker, 1974; Ebert *et al.*, 1991; Smale & Cowley, 1992; Platell *et al.*, 1998) and, at water depths greater than 500 m, deep-sea species such as the dogfish *Centroscymnus coelolepis* and the hound shark *Galeus melastomus* are important predators (Carrasón *et al.*, 1992). Members of the family Carcharhinidae are amongst the most abundant and important predators in the mangroves and shallow regions of estuaries (Salini *et al.*, 1991; Simpfendorfer, 1998).

Studies on the diets of various species of elasmobranchs have often shown that, even though they may feed on a similarly wide range of prey, the proportions of these prey items can vary greatly between species and also sometimes between the mature females and males of the same species, as is particularly the case with rajid rays and carcharhiniform sharks (see *e.g.* Holden & Tucker, 1974; Talent, 1982; Ajayi, 1982; Smale & Cowley, 1992; Platell *et al.*, 1998). The diets of elasmobranchs have also been shown to undergo size-related changes, with, for example, the larger individuals of a species ingesting a greater amount of teleosts and—or large crustaceans than the smaller individuals

(e.g. McEachran *et al.*, 1976, Ajayi, 1982; Platell *et al.*, 1998). The potential for competition for similar food resources between co-occurring species is often reduced through partitioning of prey items, as has been shown to be the case with urolophids in south-western Australia (Platell *et al.*, 1998). Such food partitioning has also been recorded among sympatric, morphologically-similar sharks, e.g. of the families Hemigaleidae and Carcharhinidae (Stevens & McLoughlin, 1991).

1.5 Determination of age in elasmobranchs

The majority of age determinations undertaken on teleost fish have been based on counts of the number of annually-deposited growth zones on hard bony structures, such as otoliths and/or scales (e.g. Campana & Neilson, 1985; Hyndes *et al.*, 1992; Hyndes & Potter, 1996). In comparison, elasmobranchs possess minute otoliths that are unsuitable for ageing purposes. However, Ridewood (1921) demonstrated that the vertebral centra of most elasmobranchs contained growth zones that were comparable with those on the hard structures of teleost fishes. Counts of such growth zones in vertebral centra now represent the most common method for determining the age of elasmobranchs (e.g. Branstetter, 1987a, b; Cailliet & Radtke, 1987; Cailliet, 1990; Cailliet & Tanaka, 1990; Simpfendorfer *et al.*, 2000). In the case of the spiny dogfish *Squalus acanthias*, the concentric growth zones on sectioned dorsal fin-spines were used as an alternative for ageing (see Holden & Meadows, 1962; Beamish & McFarlane, 1985). However, since the majority of sharks do not possess such spines, this method can only be applied to a minority of elasmobranch species. Moreover, although a large number of batoids possess caudal spines, these structures have been found, in some species, e.g. the Atlantic stingray *Dasyatis sabina* and the round stingray *Urolophus halleri*, to be capable of regeneration or to be shed and

regrown seasonally, and thus they cannot be used to provide a reliable estimate of the age of these species (Russell, 1955; Teaf, 1987).

The alternating pattern of concentric opaque and translucent zones in the vertebral centra of elasmobranchs reflects different levels of mineralisation of the centra throughout the year. The opaque zones are heavily mineralised, through the presence of high concentrations of calcium and phosphorus, whereas the translucent zones are less mineralised (Branstetter, 1987b; Yudin & Cailliet, 1990). The heavily mineralised opaque zones are formed either due to the diet becoming rich in calcium during a particular time of the year or, as with some migratory species, to an increase in the unloading of calcium from the plasma to the vertebrae during inshore migrations at a certain period of the year (Yudin & Cailliet, 1990).

For ageing purposes, it is essential to validate that the opaque (or alternatively the translucent) zones that are formed in hard structures and used for determining the age of a species are formed annually (Beamish & McFarlane, 1983). Marginal increment analysis is one of the most commonly adopted and reliable techniques for verifying that a new growth zone is formed annually in both teleosts (see *e.g.* Hyndes *et al.*, 1992; Hyndes & Potter, 1996; Maceina & Betsill, 1987; Fairclough *et al.*, 2000) and elasmobranchs (see *e.g.* Branstetter, 1987a; Natanson *et al.*, 1995; Simpfendorfer *et al.*, 2000; White *et al.*, 2001, 2002). However, Campana (2001) stated that although marginal increment analysis is a valuable method for age validation, it is also the most difficult method to carry out properly and requires sufficient rigour to be accurate. In the case of elasmobranchs, the marginal increment is the distance from the outer narrow growth zone to the periphery of the centrum. If the opaque and translucent zones form annually, the marginal increment will decline only once during the year (Hyndes *et al.*, 1992; White *et al.*, 2001, 2002). An alternative method for validating that growth zones are formed annually involves the use of

chemical tagging, whereby the fish to be aged is firstly injected with a hard-tissue marker, *e.g.* oxytetracycline hydrochloride, which is rapidly deposited in the actively growing regions near the periphery of the centra. When the vertebrae are removed and prepared from such tagged and recaptured individuals (in the wild or in captivity), after a known period of time, the numbers of zones deposited since injection of oxytetracycline are recorded (see *e.g.* Holden & Vince, 1973; Kusher *et al.*, 1992). This number should correspond to the number of years between tagging and recapture if the opaque zone is formed annually.

Elasmobranchs often undergo a substantial amount of their growth prior to parturition. For example, the females and males of the urolophids *Urolophus lobatus*, *Trygonoptera personata* and *Trygonoptera mucosa* were found to attain between 38.7 and 49.3% of their disc widths at their maximum observed ages by the time of parturition (White *et al.*, 2001, 2002). Thus, von Bertalanffy growth curves constructed using the age at parturition as age 0, as has traditionally been the case with elasmobranchs (Branstetter, 1987a, b; Simpfendorfer, 1993; Lessa *et al.*, 1999), does not include a substantial part of the overall growth of the species. Hence, the studies on the *Urolophus* and *Trygonoptera* species explored whether it was possible to use a single smooth, monotonic curve to provide a good description of growth of the females and males of these species throughout the whole of their pre- and postnatal life. Although the von Bertalanffy growth curve fitted the latter data relatively well in the case of the two *Trygonoptera* species, the use of the four parameter Schnute (1981) growth equation significantly improved the fit to the same data (White *et al.*, 2002).

1.6 Reproductive biology of elasmobranchs

The majority of the characteristics typical of elasmobranch reproduction, *e.g.* type of sex determination, low ovarian fecundity, origin of reproductive tracts and gonadogenesis, resemble more closely those of amphibians and amniotes than those of teleosts (Wourms, 1977; Dodd, 1983). In contrast to the broadcast spawning of many teleosts, in which vast quantities of eggs and sperm are released simultaneously into the water column, fertilisation in elasmobranchs occurs internally (Luer & Gilbert, 1991).

Although elasmobranchs have paired, symmetrical ovaries, only the right ovary becomes functional in most genera, *e.g.* *Carcharhinus*, *Galeus*, *Mustelus* and *Sphyrna* (see *e.g.* Wourms, 1977; Castro, 1996; Hazin *et al.*, 2001). In some other groups, both ovaries become functional, *e.g.* skates and dogfish (see *e.g.* Castro *et al.*, 1988; Teshima & Tomonaga, 1986), whereas only the left ovary becomes functional in the majority of rays, *e.g.* *Urolophus* and *Dasyatis* (see *e.g.* Babel, 1967; Wourms, 1977; Dodd, 1983). Although only low numbers of oocytes are produced by elasmobranchs, they contain extensive yolk reserves. The mature oocytes are discharged from the functional ovary (or ovaries) directly into the body cavity, from where they are transported to the oviducal gland via the ostium (or ostia) and then into the corresponding uterus (or uteri) via a connecting isthmus (Wourms, 1977). Some of the oocytes produced in the ovary may become atretic, *i.e.* the oocytes form veins and become dark golden in colour, and will subsequently be reabsorbed (Babel, 1967; Lenanton *et al.*, 1990). The oviducal gland is responsible for secreting the egg case in oviparous and some viviparous species and, in some species, *e.g.* the Australian sharpnose shark *Rhizoprionodon taylori*, blue shark *Prionace glauca* and chain dogfish *Scyliorhinus retifer*, acts as a site for sperm storage until ovulation occurs (Pratt, 1988; Simpfindorfer, 1992; Pratt & Tanaka, 1994).

Spermatozoa, which are produced in the testicular lobes of the paired testes, pass through the male accessory ducts, derived from the Wolffian duct, and into the epididymis and finally the ductus deferens (Callard *et al.*, 1988). The posterior region of the ductus deferens is enlarged and forms the seminal vesicles, which are the sites of sperm storage prior to copulation (Callard *et al.*, 1988). Sperm is transferred from the male to female via the claspers, which are modified pelvic fins that contain well-developed cartilaginous elements and are therefore rigid in mature male elasmobranchs (Wourms, 1977). Since the length of the claspers increases rapidly at maturity, after which the growth of the claspers asymptotes, the relationship between the length of the claspers and body size is commonly used to determine the size at which male elasmobranchs attain maturity (Castro *et al.*, 1988; Capapé *et al.*, 1990; Stevens & McLoughlin, 1991). Although both of the claspers are functional, only one is inserted into the female cloaca during copulation.

The two major modes of reproduction in elasmobranchs are oviparity and viviparity (Luer & Gilbert, 1991). Both of the ovaries of oviparous species, *i.e.* all skates and some sharks that inhabit benthic littoral habitats, produce oocytes that, after release from the ovaries, are fertilised in the oviducal gland and then immediately become encased in a tough, collagenous membrane, which acts as a protective case once the egg is released into the environment (Luer & Gilbert, 1991). The majority of oviparous species, *e.g.* skates and some carcharhinoids, deposit their eggs immediately and embryos hatch from the egg case after *ca* 15 months, whereas other species, *e.g.* some orectoloboids and carcharhinoids, deposit their eggs after an extended time and hatching thus occurs after only a relatively short period of time (Compagno, 1990).

The majority of elasmobranchs are viviparous, *i.e.* embryonic development occurs *in utero*, and this mode of reproduction is divided into ovoviviparity, *e.g.* squatinoids, rhinobatoids and torpedinoids (see Dodd, 1983; Compagno, 1990; Abdel-Aziz *et al.*, 1993)

and placental viviparity, *e.g.* carcharhinoids and sphyrnids (Hazin *et al.*, 1994; Castro & Mejuto, 1995; Joung & Chen, 1995). In ovoviviparous species, development of the young relies on yolk reserves, *i.e.* they are lecithotrophic. There are also two forms of specialised ovoviviparity, namely oophagy and aplacental viviparity (Wourms, 1977; Dodd, 1983). Oophagy occurs in the lamnoids and alopoids, where the young absorb the yolk sac in a short period and then feed on oocytes continually produced by the females. The young also sometimes devour other embryos, which often results in only one large embryo eventually being present in a uterus, as occurs for example with the grey nurse shark *Carcharias taurus* (Wourms, 1977; Dodd, 1983; Compagno, 1990). In aplacental viviparous species, *e.g.* urolophids, dasyatids and myliobatids, the embryos also absorb the yolk reserves at an early stage, after which extensions of the uterine mucosa, *i.e.* trophonemata, become enlarged in a hormonal response and release histotroph (uterine milk) which is absorbed by the developing embryo (Hamlett *et al.*, 1993, 1996). The gestation period in these species ranges from three to twelve months (Babel, 1967; Struhsaker, 1969; White *et al.*, 2001, 2002).

In placental viviparous elasmobranchs, the embryo ceases to depend on yolk at a very early stage and the depleted yolk sac forms a placental connection to the uterine wall (Hamlett *et al.*, 1993). This connection allows the developing embryos, which are often found in uterine compartments, to exchange oxygen, nutrients and respiratory wastes. The gestation period in these species normally lasts nine to twelve months, with, on average, six to fourteen young being produced (Hamlett *et al.*, 1993; Hazin *et al.*, 1994).

1.7 Elasmobranch fisheries

The exploitation of elasmobranchs is becoming of increasing concern throughout the world. This is reflected in the development by the Food and Agricultural Organisation (FAO) of

the United Nations of an International Plan of Action for sharks, which requests that countries with elasmobranch fisheries provide assessments of these resources and develop management procedures to protect threatened or exploited species or populations. The IUCN's Species Survival Commission Group has also formed a Shark Specialist Group (SSG), which is preparing a global Action Plan for the conservation and management of sharks (Stevens *et al.*, 2000). The reason for this concern over shark and ray fisheries worldwide relate to the susceptibility of elasmobranchs to exploitation as a result of their life-history characteristics. Sharks and rays typically have a slow growth rate, low fecundity and long life spans, and attain maturity late, which make them particularly susceptible to increasing fishing pressure (Stevens *et al.*, 2000). Thus, in comparison with most teleost species, which have a high fecundity that enables them to recover relatively rapidly from overfishing, elasmobranchs require a far longer period of time to recover from such exploitation. This is a major concern, together with the fact that the reported catch of elasmobranchs is only about half that of the estimated global catch (Bonfil, 1994; Rose, 1996). For example, although the reported global chondrichthyan landings in 1995–1996 were 760 000 tonnes, it was probably closer to 1.5 million tonnes (Bonfil, 1994; Stevens *et al.*, 2000). Indonesia and India have the largest annual landings of chondrichthyan fishes, with the totals for these two countries in 1996, being *ca* 100,000 and *ca* 70,000 tonnes, respectively (Stevens *et al.*, 2000).

The serious decline in rajid populations in some parts of the world due to overfishing provides an excellent example of the vulnerability of elasmobranchs to increased fishing pressures. Rajids have long formed a large component of the demersal fisheries in Irish and British waters (Steven, 1932). In the Irish Sea, rajid catches in the trawl fishery have declined seriously over the last 20 years, and one species, the common skate *Dipturus batis*, has been extirpated from these waters (Brander, 1981; Fahy, 1989).

Deep-water elasmobranchs, and predominantly squaloid sharks, are also commercially important in many areas of the world. Squaloid sharks have very low fecundities (*e.g.* *Centrophorus granulosus*) gives birth to one young after a 24 month gestation period, and very long lifespans, with some species living for up to 70 years (Beamish & McFarlane, 1985; Wilson & Seki, 1994; Guallart & Vicent, 2001; Clarke *et al.*, 2001, 2002). These characteristics make squaloid species extremely vulnerable to overexploitation and further highlight the need by managers for reliable biological data for those elasmobranchs that are commonly landed in such fisheries.

1.8 The Shark Bay World Heritage Area

Shark Bay is located on the central west coast of Australia and is one of only fourteen World Heritage areas in the country (Anon, 2001). The Shark Bay World Heritage region covers approximately 2.2 million ha, extending from the northern end of Bernier Island (24° 36'S, 113° 41'E) to the southern end of Freycinet Harbour (26° 36'S, 113° 41'E), of which the marine waters constitute about 71% (Francesconi & Clayton, 1996). The marine region forms a large shallow embayment covering approximately 13 000 km², that is bounded by Bernier, Dorre and Dirk Hartog Islands and the Edel Land Peninsula to the west, and is divided into two gulfs by the Peron Peninsula (Walker *et al.*, 1988) (see Fig. 2.1 in Chapter 2). The bay has an average depth of 9 m and reaches a maximum depth of 29 m (Marsh, 1990).

Shark Bay contains the most extensive seagrass meadows that have been found anywhere in the world (Walker, 1990). These seagrass meadows, which cover *ca* 4000 km², exert a significant effect on the hydrology of the bay. They stabilise the substrate and facilitate sediment accumulation, leading to the development of a large number of banks that restrict the circulation of water within the gulfs and result in the development of a

pronounced salinity gradient (Hagan & Logan, 1974; Walker, 1990). Additional factors, such as high evaporation rates, low freshwater input, restricted tidal flow and little oceanic influence, have also contributed to this gradient and have ultimately resulted in the formation of hypersaline regions (>60‰) at the southern ends of the western and eastern gulfs (Walker, 1990).

Shark Bay is located near the northern limit of a transition region between temperate and tropical marine fauna, which accounts for its high diversity of fish and that these fish are predominantly of tropical origin (Hutchins, 1990). The bay also contains one of the largest populations of dugong (*Dugong dugon*) found anywhere in the world, with the population size being estimated to be *ca* 10 000 (Anon., 1996).

1.9 The Indonesian archipelago

The Republic of Indonesia is the most expansive archipelago in the world, consisting of more than 13 000 islands, most of which are uninhabited. This country, which has a tropical climate, straddles the equator and stretches for almost 5 000 km from Sabang in northern Sumatra (5°38'N, 94°44'E) to near Merauke on the Irian Jaya-Papua New Guinea border (141°37'E), and for 1 770 km south to the island of Roti off West Timor (13°33'S) (Encyclopaedia Britannica, 1993). The country consists of five main islands, namely Sumatra, Java, Kalimantan, Sulawesi and Irian Jaya (see Fig. 2.2 in Chapter 2). The physical features of this country are unique, consisting of a complex series of shelves, volcanic mountain chains and deep-sea trenches that have been present, in geological terms, for a long period and which have resulted in Indonesia having the highest rate of generic endemism in the world (Anon., 1995). Indonesia contains the most diverse seagrass meadows in the world, with more than 12 species, the greatest areas of mangroves in the

world and extensive regions of coral reefs, *i.e.* they cover an area of more than 7 500 km² (Anon., 1995). Such an expanse of marine waters and diversity of habitats has contributed to this country having one of the richest elasmobranch faunal assemblages in the world (see *e.g.* Gloerfelt-Tarp & Kailola, 1984; Last & Stevens, 1994; Carpenter & Niem, 1998, 1999).

The declaration of the Indonesian Exclusive Economic Zone (EEZ) in 1983 gave the country control of more than 5.4 million km² of marine waters (Wibowo & Susanto, 1995; Carpenter, 1998). The total fisheries catch for Indonesia in 1995 was more than 3.2 million tonnes, whereas that for Australia was only 214 196 tonnes (Carpenter, 1998).

1.10 Broad aims of the study

The broad aims of this study were as follows.

1. Determine the relative abundance and distribution of elasmobranchs in different habitats in a shallow bay (Herald Bight) on the Peron Peninsula in Shark Bay, and to elucidate which of those species use these habitats as nursery areas.
2. Determine the dietary compositions of the most abundant species of elasmobranchs in Herald Bight and whether those compositions change with increasing body size and time of year and, if so, how.
3. Use the data produced by 1 and 2 to determine the extent to which the spatial and food resources of Herald Bight are partitioned amongst the main elasmobranch species in that location.
4. Determine the size and age compositions and reproductive biology of the nervous shark *Carcharhinus cautus* in Shark Bay.
5. Fit growth curves to the lengths at age of individuals of *C. cautus*, using both the age at conception and the age at parturition as age 0.

6. Determine whether or not the conventional von Bertalanffy growth equation provides the most appropriate fit to the lengths-at-ages of individuals of *C. cautus* or whether a more complex growth equation, e.g. Schnute growth equation, is required to provide a better description of these data.
7. Determine the species and size compositions of chondrichthyans caught in target and non-target fisheries in south-eastern Indonesia and whether some of the most abundant of these species are being fished prior to reaching maturity.
8. Provide preliminary details of the reproductive biology and size compositions of three abundant dasyatid species, i.e. *Dasyatis kuhlii*, *Dasyatis zugei* and *Himantura walga*, in the Java Sea in south-eastern Indonesia and determine the age composition of *D. kuhlii*, the most abundant of these three species. Since this is only preliminary data, it has been presented in Appendix II of this thesis.
9. Construct a field guide containing keys, images and species accounts for all chondrichthyans recorded in Indonesia.

CHAPTER 2

General materials and methods

2.1 Sampling locations and regime in Shark Bay

The elasmobranchs and teleosts at three unvegetated nearshore sites (depth = 1.2–1.8 m) and one vegetated (seagrass) site (depth = 2–3 m) in Herald Bight, which is located at 25° 40'S, 113° 32' E at the north-eastern tip of the Peron Peninsula of Shark Bay (Fig. 2.1; Plate 2.1), were sampled by gillnetting at night. The first of the three unvegetated sites was situated over bare sand and was close to neither mangroves nor seagrass (Plate 2.2), whereas the second and third were adjacent to sparse (Plate 2.3) and dense mangroves (Plates 2.4, 2.5), respectively. Since the mangroves (*Avicennia marina*) in Herald Bight are found along the shore and thus in shallow water (<1 m), it was not possible, even on a high tide, to set the gillnet effectively within the mangroves. Thus, at the two sites located near to mangroves, the gillnet was set perpendicular from the shore, commencing at a distance of *ca* 3 m from the outer edges of the stands of fringing mangroves (Plate 2.6). The water depths sampled by the gillnet at these sites on each sampling occasion ranged from at least 1.2 m to *ca* 2.2 m. At the site where the fringing mangroves were dense, the gillnet was set adjacent to the entrance to a tidal inlet that contained dense stands of mangroves so that they would catch the elasmobranchs that were moving into them at high tide (water depth at high tide = 0.8–1.4 m). The fourth and vegetated site, which contained seagrass beds (*Posidonia australis*), was located 1 km offshore from the sand-seagrass transition zone and ranged from 2 to 3 m in depth.

Although each of the three unvegetated sites was sampled at least bimonthly between October 1999 and September 2001, concomitant sampling of the vegetated site had to be discontinued after July 2000, when it became apparent that gillnetting might catch dugongs (*Dugong dugon*), a protected species. The samples from each of the unvegetated nearshore sites were pooled by season, thus providing at least three replicate samples for each season during the sampling period. The composite monofilament gillnet,

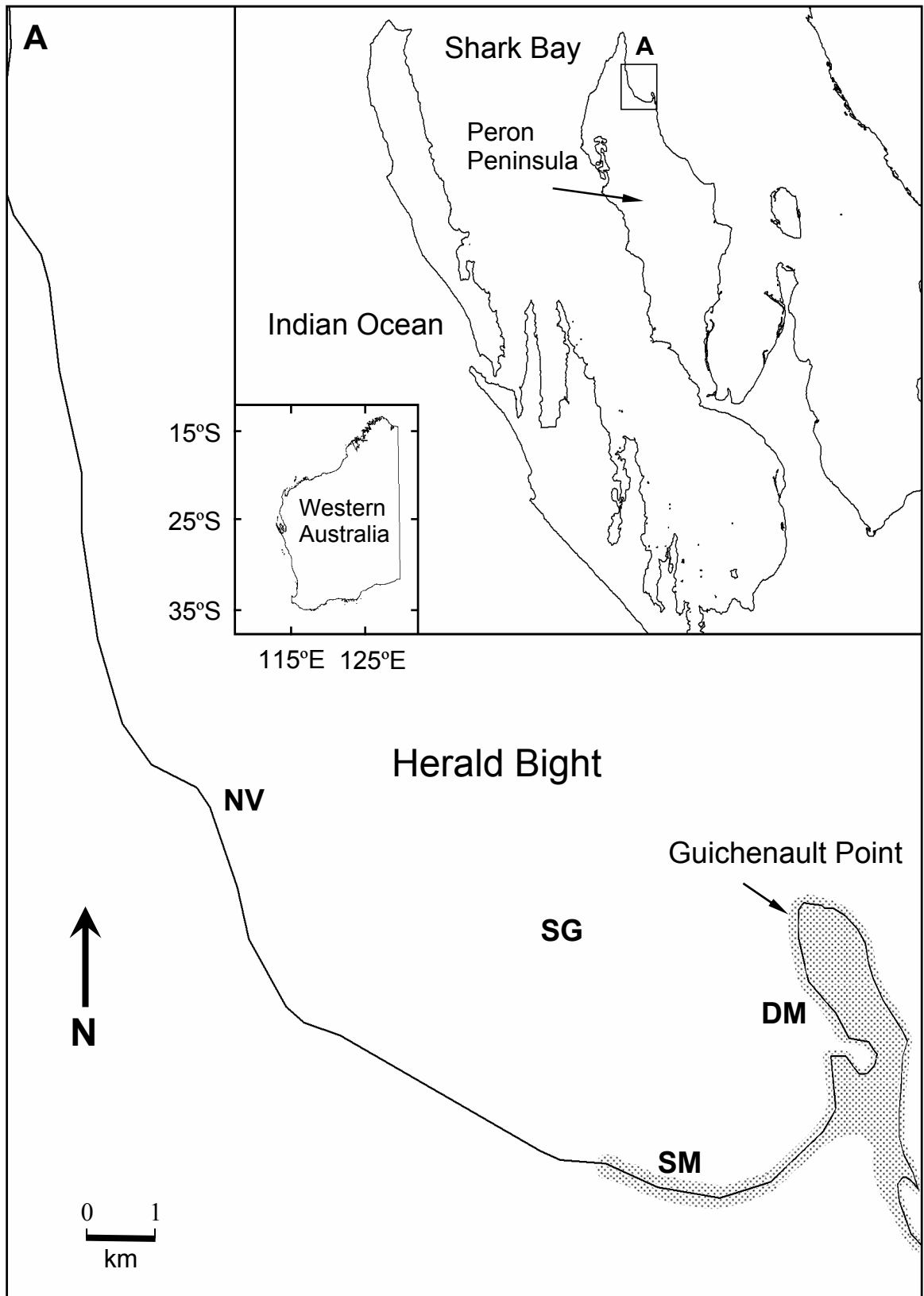


Figure 2.1 Locations of the four gill net sampling sites, *i.e.* unvegetated and with no vegetation nearby (NV), unvegetated and near sparse mangroves (SM), unvegetated and near dense mangroves (DM) and seagrass (SG) in Herald Bight at the north-eastern end of the Peron Peninsula in Shark Bay (labelled A in box). Shading represents mangrove areas.

which was set at night for 3 h at around high tide, were 2.5 m high and comprised three 30 m long panels, each containing a different mesh, *i.e.* either 100, 150 or 175 mm.

One of the three species of sharks whose diets were studied (*Carcharhinus cautus*) was also collected opportunistically by haul and seine netting, and further samples of both this species and *Negaprion acutidens* were obtained by rod and line angling during the night. Since the morphological characteristics of *Rhinobatus typus* enabled it to escape retention by gillnets, it was collected by seine netting, hand spearing and rod and line angling in the nearshore, shallow regions of Herald Bight and from a similar habitat just to the south of this bay. The mesh size in the 60 m long haul net was 100 mm, whereas those in the wings and bunt of the 21.5 m seine net were 9 and 3 mm, respectively. The water temperature (°C) and salinity (‰) were recorded at each site on each occasion that it was sampled.

The total length (to the nearest 1 mm for individuals less than 600 mm and to 10 mm for those over 600 mm in length), total body mass (to the nearest 0.1 g) and sex of each shark and ray collected were recorded in the field. In the case of males, the level of calcification of the claspers, *i.e.* not calcified, not fully calcified and fully calcified, and the length of the claspers (to the nearest 1 mm), measured from posterior of cloaca to the tip, were also recorded. Other biological procedures were also carried out where appropriate (see Chapters 3–6).

2.2 Sampling locations and regime in south-eastern Indonesian

The chondrichthyan catches at various landing sites in Indonesia were recorded on nine occasions between April 2001 and January 2003. Five landing sites were visited on the majority of sampling occasions, *i.e.* Muara Angke (Jakarta), Palabuhanratu (West Java), Cilacap (Central Java), Kedonganan (Bali) and Tanjung Luar (Lombok), one landing site

on four occasions, *i.e.* Muara Baru (Jakarta) and three landing sites on a single occasion, *i.e.* Pekalongan (Central Java), Kendari (Sulawesi) and Merauke (Irian Jaya) (see Fig. 2.2). The landing site of Kupang (West Timor) was also visited on one occasion by the two Indonesian project scientists, but, due to the limited chondrichthyan catches, *i.e.* only four species, this site was not surveyed on subsequent trips.

The fishing port of Muara Angke is located at the mouth of the Angke River on the north coast of the Jakarta Province ($6^{\circ} 08'S$, $106^{\circ} 45'E$; see Fig. 2.2) of West Java. The main fisheries operating out of Muara Angke are trawling, trapping, purse seining and both demersal and inshore pelagic gillnetting. Elasmobranchs are the target species of the demersal gillnet fishery operating out of this site (Plate 2.7) and also frequently occur as bycatch in the trawl, trap and inshore pelagic gillnet fisheries. The port of Muara Baru (Plate 2.8) is located slightly to the east of the Muara Angke landing site. The main fishery operating out of this port is pelagic longlining, but there are also some small trawl and gillnet fisheries. Although the pelagic longlining fishery primarily targets tuna, elasmobranchs are a common bycatch and are also abundant in the catches of the gillnet fishery operating out of this site.

Palabuhanratu is a small fishing town located on the southern coastline of West Java, almost directly south of Jakarta (Plate 2.9; Fig. 2.2). The predominant fishery operating out of this location is the combination of gillnetting for tuna and associated longlining for sharks. There are also some minor fisheries operating out of Palabuhanratu, including purse seining, deep-water demersal longlining and droplining, hand lining and gillnetting in shallow regions and stationary light traps (bagan). Sharks and rays, which are the target species in the deep-water fishery, are also occasionally caught as bycatch in the other fisheries. The fishing harbour of Cilacap (Plate 2.10) is located on the southern coast

of Central Java, just east of the border with West Java (Fig. 2.2), and has the only natural harbour on Java's south coast. The main fishery that operates out of Cilacap is pelagic gillnetting and longlining for tuna which involves a high bycatch of pelagic sharks. Other smaller fisheries also exist, including one for prawns, demersal trammel-netting for small teleosts, with a small bycatch of batoids, and deep-water demersal longlining for squalid sharks. Pekalongan, which is located on the north coast of Central Java (Fig. 2.2), has a relatively large fishing port. There is a large purse seine fishery for small pelagic teleosts at this port with several other minor fisheries also occurring, but no fisheries directly targeting elasmobranchs.

The fishing village of Kedonganan is located in Jimbaran Bay on the west coast of southern Bali (Plate 2.11; Fig. 2.2). Teleosts, which form the major component of the fishery at this location, are caught by a variety of methods, *e.g.* purse seining, drop-longlining and gillnetting, in a variety of habitats, such as shallow demersal, coral reef and inshore pelagic waters. Elasmobranchs are targeted by demersal gillnetting as well as demersal longlining in depths greater than 60 m. Tanjung Luar is located on the east coast of Lombok (Fig. 2.2) and is one of the main landing sites on the island (Plate 2.12). The main fisheries operating out of this port are pelagic and deep-water longlining and inshore pelagic purse seining, with a variety of other minor fisheries also operating out of this site. Elasmobranchs, which are the target species in the pelagic and deep-water longlining fisheries at this site, are also frequently caught by other fishing methods, *e.g.* handlining. Kendari is the capital of the province of South-East Sulawesi and is located on its east coast (Fig. 2.2). Although there are several landing sites at Kendari, very few elasmobranchs are landed as the shark and ray fisheries operating from these sites unload their catches at sea for immediate export overseas (Usman Rianse, pers. comm.). Merauke is the easternmost town in Indonesia and is located on the south coast of Irian Jaya (Papua), *ca* 40 km from

the Papua New Guinean border (Fig. 2.2). The main fishery operating from the fishing port in Merauke is trawling. However, since the catch is unloaded at sea into a larger ship for direct export (Plate 2.13), the catch cannot be observed. Elasmobranchs are also targeted by demersal gillnet fishers operating in the Arafura Sea, but these are also unloaded at sea. Locally, along the Merauke beach communities (Plate 2.14), fishers use gillnets set from either the shore or slightly offshore from the coast to target teleosts but also catch a small number of sharks. Seine net fishermen operating from the shore target penaeid prawns but also catch a small number of rays.

CHAPTER 3

**Habitat partitioning among four species of elasmobranch in nearshore,
shallow waters of a subtropical embayment in Western Australia**

3.1 Introduction

Elasmobranchs, and particularly members of the Carcharhinidae, are very abundant in subtropical and tropical waters throughout the world, including those of Australia (Compagno, 1984). Indeed, sharks alone comprised as much as 78% of the total catch of the Taiwanese surface gillnet fishery that operated in northern Australian waters between 1974 and 1986 (Stevens & Wiley, 1986). An example of the crucial role played by sharks in certain trophic systems is illustrated by the large contribution that they make to the total biomass of predators in the Gulf of Carpentaria in northern Australia (Blaber *et al.*, 1989).

Many shark species use the nearshore waters of estuaries and embayments as nursery areas (Springer, 1967; Blaber *et al.*, 1985, 1989; Lyle, 1987; Simpfendorfer & Milward, 1993). For example, the juveniles of the Australian sharpnose shark *Rhizoprionodon taylori*, milk shark *Rhizoprionodon acutus*, spot-tail shark *Carcharhinus sorrah* and Australian blacktip shark *Carcharhinus tilstoni* each employ, for this purpose, Cleveland Bay on the north-eastern coast of Australia at certain times of the year (Simpfendorfer & Milward, 1993). Although most of the elasmobranch species found in nearshore waters only use those waters as nursery areas, a few spend the whole of their life cycle in those waters, *e.g.* the nervous shark *Carcharhinus caudus* in northern Australia (Lyle, 1987).

Nursery areas, and particularly those where there is some form of vegetation, presumably provide juvenile sharks and rays with protection from predation, *e.g.* the lemon shark *Negaprion brevirostris* (Branstetter, 1990). They are also productive and thus provide the recently-born individuals of elasmobranchs with an abundant source of food. Although the use of the same nursery areas by a number of species increases the opportunity for competition for food resources, the mangrove areas of subtropical and tropical estuaries are productive and therefore capable of supporting large populations of the prey on which

elasmobranchs feed (Robertson & Duke, 1987). Thus, the shark species that employ Cleveland Bay as a nursery area mainly exploit the large teleost and prawn populations present in the mangroves and seagrass meadows of this embayment (Simpfendorfer & Milward, 1993).

Several studies have described the composition of elasmobranch assemblages in inshore waters of the northern hemisphere (*e.g.* Snelson & Williams, 1981; Talent, 1985; Ebert, 1986). However, none of these studies included a statistical analysis of whether the compositions of these various assemblages differed significantly among habitats and during the year. Furthermore, although Blaber *et al.* (1989) recorded the species compositions and biomasses of teleosts and elasmobranchs in five habitats in a mangrove estuary in northern Australia, their study focused mainly on the former taxa as this was by far the most abundant.

Despite the ecological importance of Shark Bay, only one study has used samples collected at regular intervals throughout the year to analyse the composition of the fish community within the two main gulfs of that embayment (Fig. 2.1) (Travers & Potter, 2002). Furthermore, that study employed a small otter trawl that was not appropriate for catching elasmobranchs. Two other studies investigated the fish faunas of two regions at different times of the year, but the sampling method, *i.e.* seine netting, was not designed to catch sharks or rays (Lenanton, 1977; Black *et al.*, 1990). The paucity of data on the fish faunas of this World Heritage area reflects the difficulties posed to sampling such a remote environment at regular intervals. Although there are essentially no ecological data on the elasmobranch fauna of Shark Bay, catches obtained using setlines have demonstrated that the tiger shark *Galeocerdo cuvier*, dusky shark *Carcharhinus obscurus* and sandbar shark *Carcharhinus plumbeus* are the most common of the large elasmobranch species in the more offshore and deeper waters of this embayment (Simpfendorfer *et al.* 2001a, b;

McAuley, WA Dept. Fisheries, unpubl. data). In contrast, the nervous shark *C. cautilus*, lemon shark *Negaprion acutidens*, milk shark *R. acutus* and giant shovelnose ray *Rhinobatus typus* are abundant in certain nearshore waters of this large water body.

The aim of the present study was to test the following hypotheses. 1) The shallow protected waters of Herald Bight, a bay covering an area of approximately 67 km² on the north-eastern tip of the Peron Peninsula in Shark Bay (Fig. 2.1), is used as a nursery area by certain elasmobranch species. 2) The various elasmobranch species are partitioned, to a certain degree, among the main habitat types in these nearshore waters, *i.e.* unvegetated with no seagrass or mangroves nearby, unvegetated but adjacent to sparse mangroves, unvegetated but adjacent to dense mangroves, and vegetated with seagrass. 3) The number of species and relative abundance of elasmobranchs are greater in seagrass and regions adjacent to mangroves than in areas over bare sand where no vegetation is present nearby and food and protection will thus be less available. 4) The composition of the elasmobranch assemblages in the nearshore waters of Shark Bay change throughout the year as a result of differences in the times when the various species use these waters. Finally, data are provided on the teleosts caught in the gillnets and these are included with the elasmobranchs in one of the multivariate analyses to ascertain whether both fish taxa continue to form similar groupings according to habitat type as those produced by elasmobranchs on their own.

3.2 Materials and methods

3.2.1 Sampling location and regime

Details of the sampling regime and gillnets used to catch elasmobranchs in Herald Bight are given in Chapter 2. Note that only those elasmobranchs that were caught by gillnetting in

Herald Bight were used for this part of the study on spatial resource partitioning so that the multidimensional scaling ordinations (see later) would be performed on comparable species composition data. A record was kept of any shark that possessed an umbilical scar on its ventral surface. Note that, since all rays, except for the rhinobatid *Rhinobatus typus*, were released live immediately after their removal from the net, neither their size nor body mass were recorded. The number of each fish species and total biomass of each shark species caught in the three nearshore, unvegetated sites and the single seagrass site were recorded.

3.2.2 Analyses

The number of species and individuals at each of the four sampling sites, *i.e.* unvegetated with no vegetation present nearby, unvegetated near sparse mangroves, unvegetated near dense mangroves and vegetated with seagrass, in each corresponding season of the different years were grouped together to provide a number of replicates for each site (habitat type) in each season of the year. As the gillnet was always set for 3 hours on each sampling occasion, the number of individuals caught on each set corresponds to a catch rate, *i.e.* number of fish caught $\text{net}^{-1} 3\text{h}^{-1}$. Since the seagrass meadows were not gillnetted during the warmest months, the number of replicate samples for this habitat type was less than for the three unvegetated habitat types. For the above reasons, analyses were performed firstly on the data obtained for the three unvegetated sites throughout the whole study and then on the data obtained from these three sites and the seagrass site on those more limited occasions when all four sites were sampled.

The results of plots of the log of the standard deviation against the log of the mean for the number of species and individuals of elasmobranchs in the three unvegetated sites showed that, prior to subjecting these biotic variables to Analysis of Variance (ANOVA), the former required no transformation whereas the latter required a fourth root

transformation (see Clarke & Gorley (2001) for rationale for this approach). When the same approach was adopted for the number of elasmobranch species and number of elasmobranchs in the three unvegetated sites and single seagrass site during autumn, winter and spring, it was found that they required square root and fourth root transformations, respectively. Following their transformations, the number of species and number of individuals at the three unvegetated sites in each season were both subjected to a two-way ANOVA. The independent variables in the ANOVA, *i.e.* habitat type and season, were considered fixed factors (Underwood, 1997). However, the number of replicates for the number of elasmobranch species and number of elasmobranchs at the three unvegetated sites and single seagrass site, when each of these sites was sampled in the same month, were too low to explore the influence of season separately. Thus, the data for those two biotic variables at each of the four habitat types were subjected to a one-way ANOVA, in which the data for season were pooled. When ANOVAs showed that there were significant differences between either the number of species and/or number of individuals for a variable (habitat, season), Scheffé's *a posteriori* test was employed to determine where the differences resided. Note that, when data were transformed for the purposes of ANOVA, it is the back transformed data that are presented in the figures and text.

The mean numbers of the various elasmobranch species caught at each site in each season, and subsequently of the various elasmobranch and teleost species collectively, were ordinated using the non-metric multidimensional scaling techniques described in the PRIMER v5.2.2 package (Clarke & Gorley 2001). Prior to ordination, the mean numbers of the various species were fourth root transformed, and a similarity matrix constructed using the Bray-Curtis similarity coefficient. One-way analyses of similarities (ANOSIM) were employed to test whether the species composition in the samples collected from the four sites and in each season were significantly different (Clarke, 1993). Multivariate dispersion

(MVDISP) was used to determine the extent of the dispersion of points representing the samples in each *a priori* group (Somerfield & Clarke, 1997) and similarity percentages (SIMPER) were used to determine which species were responsible for any dissimilarities in the species compositions of the different groups (Clarke, 1993).

3.3 Results

3.3.1 Environmental variables

The mean monthly water temperatures in Herald Bight ranged from 17.2°C in mid-winter to 33.5°C in early autumn at the unvegetated sites and from 19.2°C in late winter to 27.2°C in early autumn at the seagrass site (Fig. 3.1). The mean monthly salinity at each of the three unvegetated sites and the single vegetated site each lay within the narrow range of 39.1 to 41.6‰.

3.3.2 Number, abundance and biomass of individual species and mesh selectivity

A total of 369 sharks, 13 rays and 159 teleosts were caught by gillnetting in Herald Bight between October 1999 and September 2001. These represented ten species from five families of shark, five species from four families of ray and twelve species from ten families of teleost (Table 3.1). *Carcharhinus cautus* was by far the most abundant elasmobranch species, comprising 59.9% of the total number of elasmobranchs and 42.3% of all fish caught. *Rhizoprionodon acutus* and *Negaprion acutidens* were the only other relatively abundant elasmobranch species, contributing 15.4 and 10.7%, respectively, to the

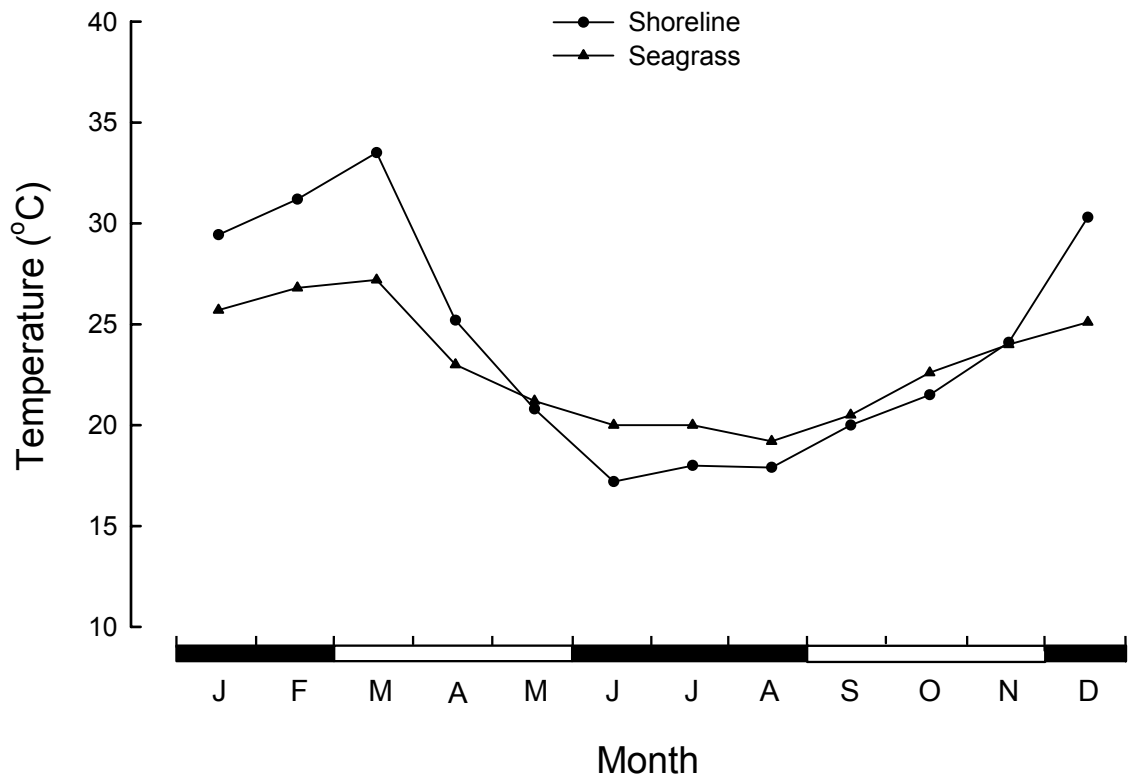


Figure 3.1 Mean monthly water temperatures at sites along the shoreline and in the seagrass where gillnetting was conducted in Shark Bay between January 1999 and September 2001. In this and subsequent Figs, the data for the corresponding months of the different years have been pooled and, on the x-axis, closed rectangles refer to summer and winter, and open rectangles to autumn and spring months.

numbers of elasmobranchs and 10.9 and 7.6%, respectively, to the numbers of all fish (Table 3.1).

Carcharhinus cautus contributed between 27.6 and 59.9% to the total catches at the three unvegetated sites, but only 4.0% to those at the seagrass site (Table 3.1). Furthermore, all of the 41 *N. acutidens* that were caught came from the three unvegetated sites. In marked contrast, all but one of the 59 *R. acutus* and all of the 12 *Carcharhinus brevipinna* and 11 *Chiloscyllium punctatum* were caught at the seagrass site (Table 3.1). Batoids were caught only at unvegetated sites.

The most abundant teleost species were *Mugil cephalus* and *Pomatomus saltatrix*, which were caught only at the three unvegetated sites, and which constituted 8.9 and 5.5%, respectively, of the total catch of all fish. A further nine species of teleost were caught in low numbers at the unvegetated sites. The single species that was caught at the seagrass site, *i.e.* *Scomberomorus munroi*, contributed 20% to the total fish catch at this site, and was not caught at the unvegetated sites (Table 3.1).

The total biomass of sharks caught during the present study was 1425 kg, of which *C. cautus* contributed 1058 kg, *i.e.* about 74% (Fig. 3.2). The next two greatest contributors were *N. acutidens* (155 kg), which was caught exclusively at unvegetated sites, and *C. plumbeus* (115 kg), which was collected only in seagrass (Fig. 3.2). The large biomass of the latter species was mainly due to the capture of one large pregnant female. None of the other shark species contributed more than 40 kg to the total mass of selachians caught at any of the three unvegetated sites collectively or at the single vegetated site (Fig. 3.2). The total lengths of the sharks caught by gillnetting ranged from 350–2190 mm, with the majority lying between 500 and 1250 mm. The sharks caught in panels with meshes of 100, 150 and 175 mm had minimum lengths of 350, 640 and 750 mm, respectively, and mean lengths \pm 95% confidence limits of 746 ± 34 , 998 ± 40 and 1037 ± 40 mm, respectively

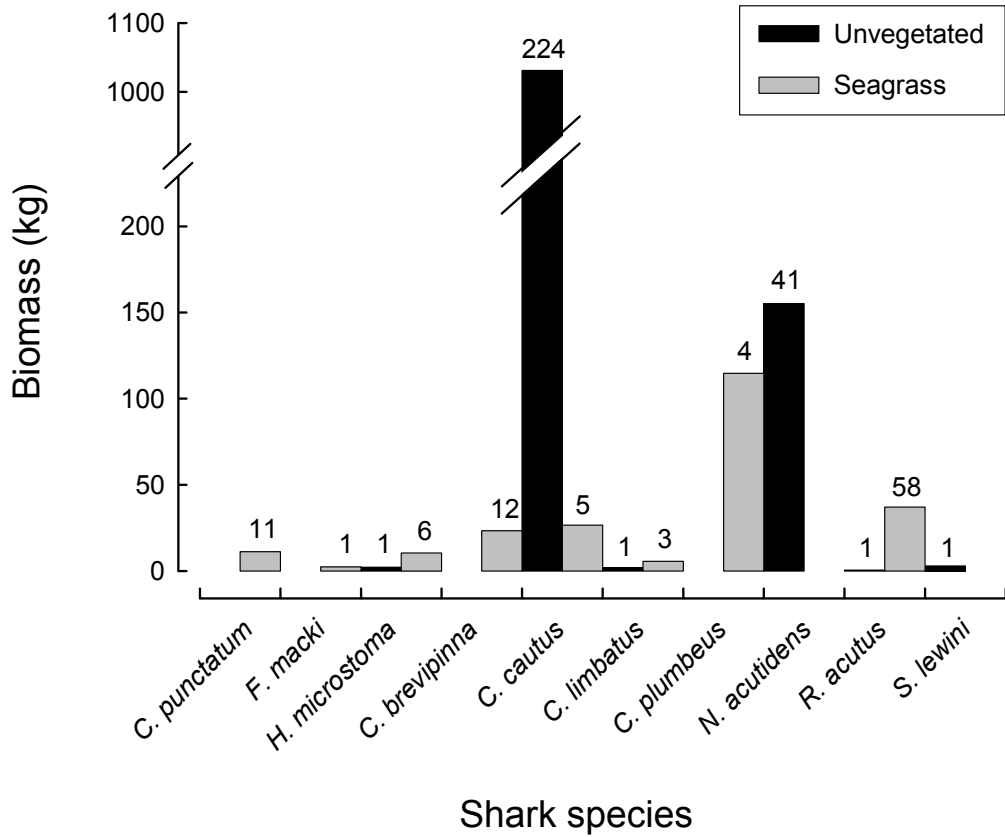


Figure 3.2 Biomass of each shark species caught in unvegetated areas and over seagrass in Herald Bight on all sampling occasions between October 1999 and September 2001. Numbers of individuals of each species are shown above bars.

(Fig. 3.3). One-way ANOVA showed that the mean lengths of elasmobranchs caught by the panels with the three meshes were highly significantly different ($P < 0.001$). Scheffé's *a posteriori* test demonstrated that the mean lengths of sharks caught by the 100-mm mesh were significantly less ($P < 0.001$) than those caught by the 150-mm and 175-mm mesh sizes and that the mean lengths of sharks retained in the latter two mesh sizes were not significantly different ($P > 0.05$). The number of sharks caught in the panel with the smallest mesh (100 mm) contributed 61% to the total catch of sharks, compared with 21 and 18% by the panels with 150-mm and 175-mm mesh, respectively.

3.3.3 Monthly occurrences and lengths of species

Although *Carcharhinus cautus* was caught in each of the ten calendar months in which sampling was carried out, recently-born individuals were found only between December and April and predominantly in December and January (Table 3.2). *Negaprion acutidens* was caught in all months sampled between October and June, with recently-born individuals being found between December and April, but it was not caught in July, August and September. Most of the *Rhizoprionodon acutus*, i.e. 55 of 59 individuals, were caught in April and July and four of these were recently born. All of the twelve *Carcharhinus brevipinna* were caught in July and all but two of these had been recently born. There was no tendency for the other species, which were obtained in low numbers, to be found collectively at one particular time of the year.

The lengths of *Carcharhinus cautus* ranged from 390 to 1330 mm, with the majority lying between 800 and 1200 mm (Fig. 3.4). The lengths of the recently-born individuals of this species lay between 390 and 490 mm. All of the *Rhizoprionodon acutus*, which ranged in length only from 350 to 770 mm, were immature, with the lengths of recently-born individuals ranging between 350 and 390 mm (Fig. 3.4). The lengths of

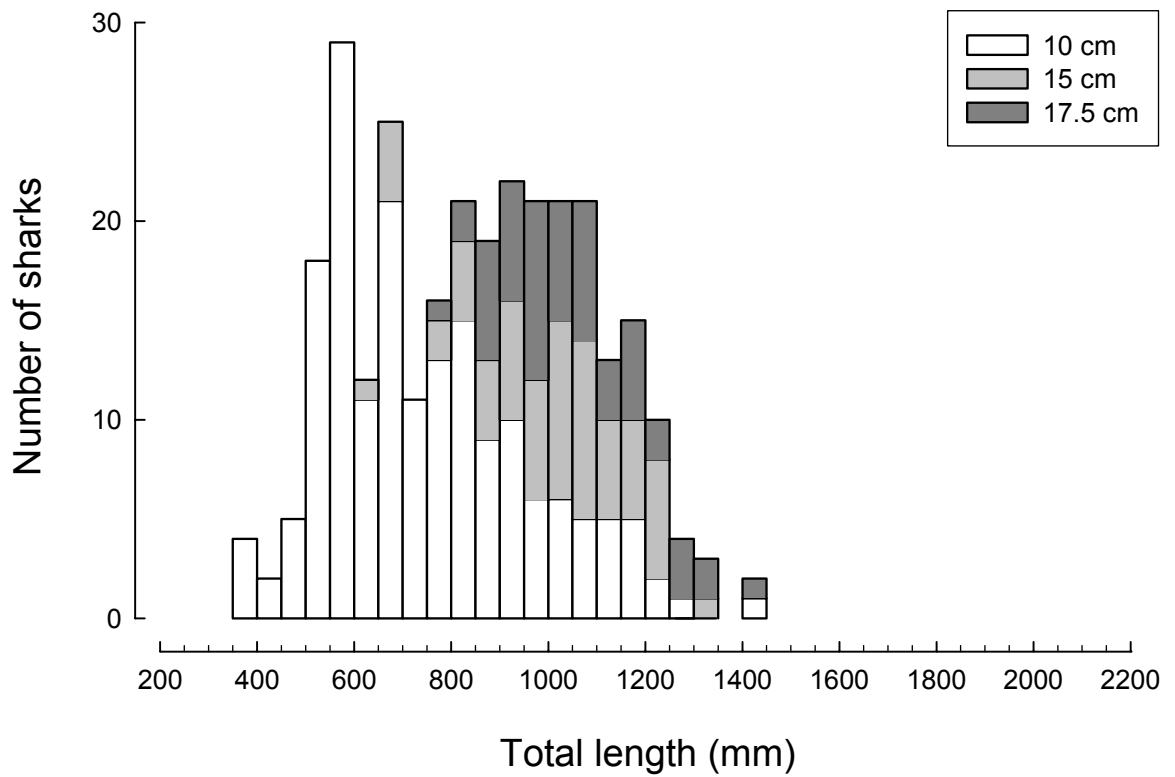


Figure 3.3 Number of individuals in each sequential 50-mm length class of shark that were caught in the three 30-m gillnet-panels with meshes of 100, 150 and 175 mm.

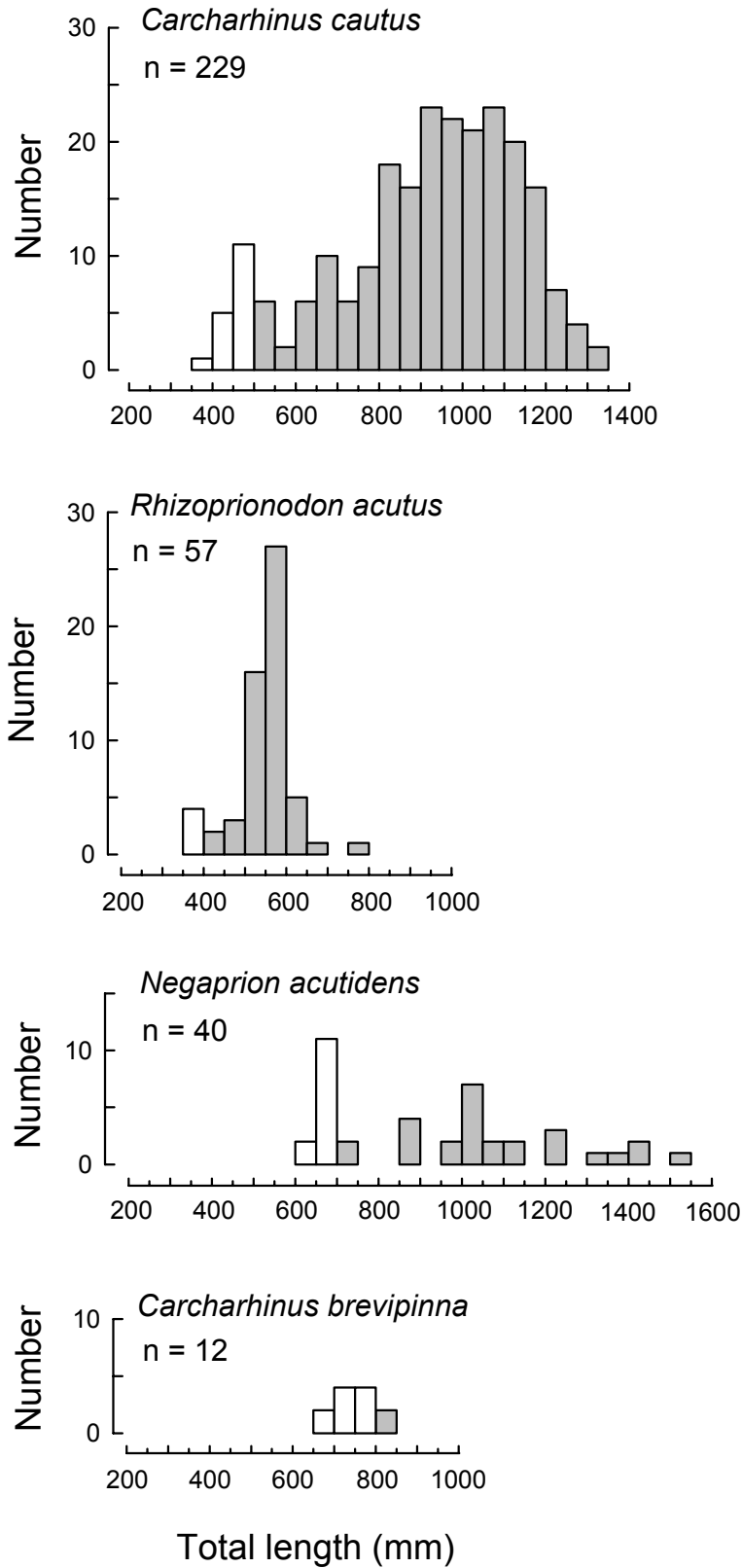


Figure 3.4 Length-frequency histograms for the four most abundant shark species caught by gillnetting in Herald Bight. White bars refer to recently-born individuals, *i.e.* with umbilical scars.

Negaprion acutidens ranged from 630 to 1510 mm, with those of recently-born individuals lying between 630 and 690 mm. The 12 *Carcharhinus brevipinna* that were caught, of which ten were recently-born, ranged in length only from 650 to 810 mm (Fig. 3.4). All of the 11 *Chiloscyllium punctatum* (length-range 550–710 mm) and the seven *Hemigaleus microstoma* (length-range 630–920 mm) were mature. Three recently-born individuals of *C. plumbeus*, with lengths 610–660 mm, and one large pregnant female of this species, with a length of *ca* 2200 mm, were caught.

3.3.4 *Numbers of species and individuals*

Two-way ANOVA showed that the mean number of species of elasmobranch caught at the three unvegetated sites differed among seasons and habitats, and that there was no significant interaction between these two factors (Table 3.3). Scheffé's *a posteriori* test demonstrated that the mean number of species caught on the different sampling occasions at the sites near dense mangroves, 1.8, and near sparse mangroves, 1.6, were both significantly greater ($P < 0.05$) than at the site with no mangroves nearby, 0.95 (Fig. 3.5). The mean number of species caught in summer, 2.1, and autumn, 2.3, were significantly greater ($P < 0.05$) than those collected in winter, 0.3, and spring, 1.0 (Fig. 3.5).

The mean number of elasmobranchs caught at the three unvegetated sites differed significantly among seasons and habitats, but there was no significant interaction between these two factors (Table 3.3). The mean number of elasmobranchs caught on the different sampling occasions at the site near dense mangroves, 7.4, was significantly greater ($P < 0.05$) than that at the site with no mangroves nearby, 0.8 (Fig. 3.5). The mean number of elasmobranchs caught in summer, 8.0, and autumn, 6.2, were significantly greater ($P < 0.05$) than in winter, 0.01 (Fig. 3.5).

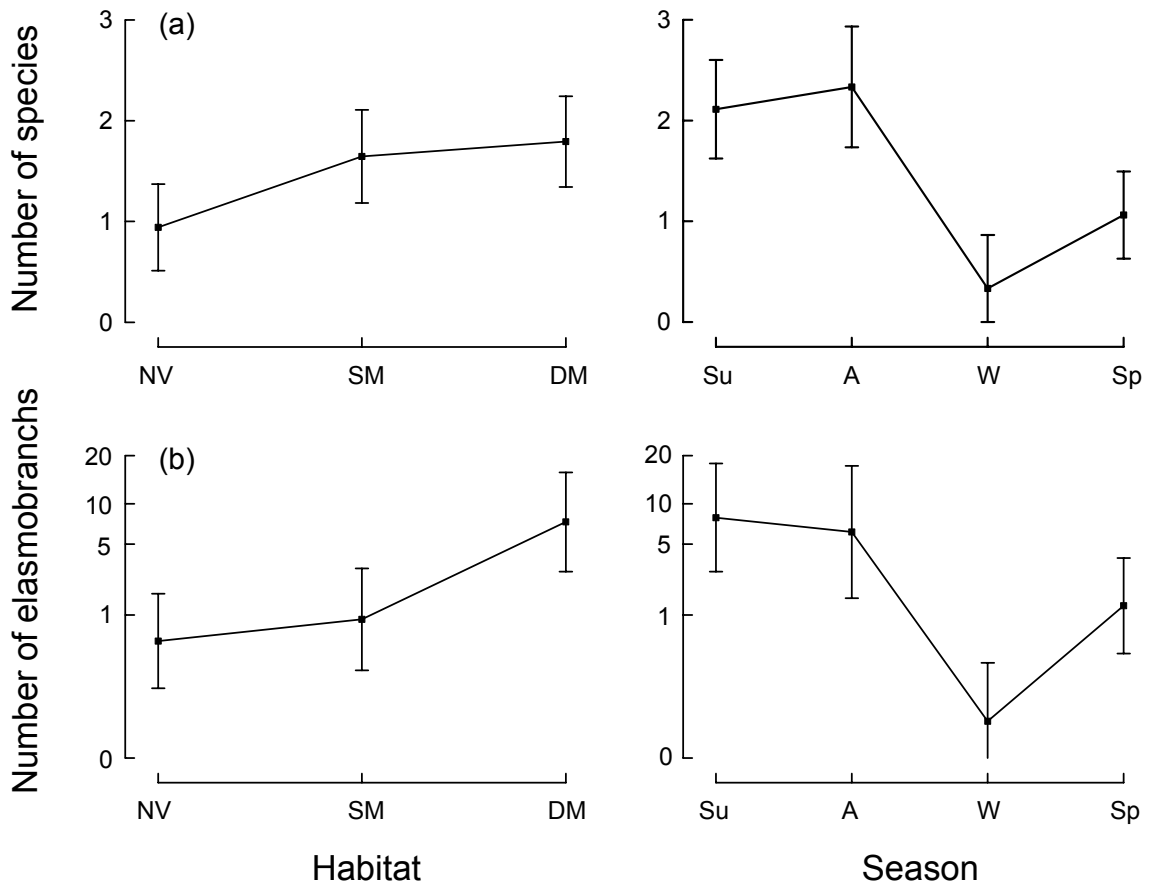


Figure 3.5 Mean \pm 95% confidence limits for (a) number of species of elasmobranch and (b) number of elasmobranchs in three unvegetated habitat types and in each season. NV, no vegetation nearby; SM, sparse mangroves nearby; DM, dense mangroves nearby. Su, summer; A, autumn; W, winter; Sp, spring.

Table 3.3 Mean squares and significance levels for (a) two-way ANOVAs of both the number of species of elasmobranch and the number of elasmobranchs caught $\text{net}^{-1} 3\text{h}^{-1}$ in each of the three unvegetated sites and (b) a one-way ANOVA of both the number of species of elasmobranch and the number of individuals of all elasmobranchs caught $\text{net}^{-1} 3\text{h}^{-1}$ on those occasions when all four habitat types were sampled. Data for the two-way ANOVAs are derived from gillnetting seasonally in Herald Bight between October 1999 and September 2001, whereas those for the one-way ANOVAs are derived from gillnetting only on those occasions when the seagrass site was sampled and have been pooled for season.

	Main effects		Two-way interactions	Residual
	Season	Habitat	Season x Habitat	
(a)	d.f. (3)	(2)	(6)	(23)
Number of species	5.53***	2.18*	0.50	0.46
Number of individuals	3.29***	2.14**	0.07	0.30
(b)		(3)		(12)
Number of species		1.77*		0.35
Number of individuals		4.07**		0.42

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

The mean number of species and mean number of elasmobranchs, employing only the data obtained on those occasions when all four habitat types were sampled, declined progressively from the seagrass site to the unvegetated site with dense mangroves and then sparse mangroves and finally to the unvegetated site with no vegetation nearby. One-way ANOVA showed that the mean number of elasmobranch species and the mean number of elasmobranchs caught on the separate sampling occasions both differed significantly among habitat types (Table 3.3). The mean number of species caught at the seagrass site, 2.9, was significantly greater ($P < 0.05$) than at the unvegetated site with no vegetation nearby, 0.1 (Fig. 3.6). The mean number of elasmobranchs caught on the separate sampling occasions at the seagrass site, 34.7, was significantly greater ($P < 0.05$) than at both the unvegetated site near sparse mangroves, 0.01, and at the site with no vegetation nearby, 0.01 (Fig. 3.6).

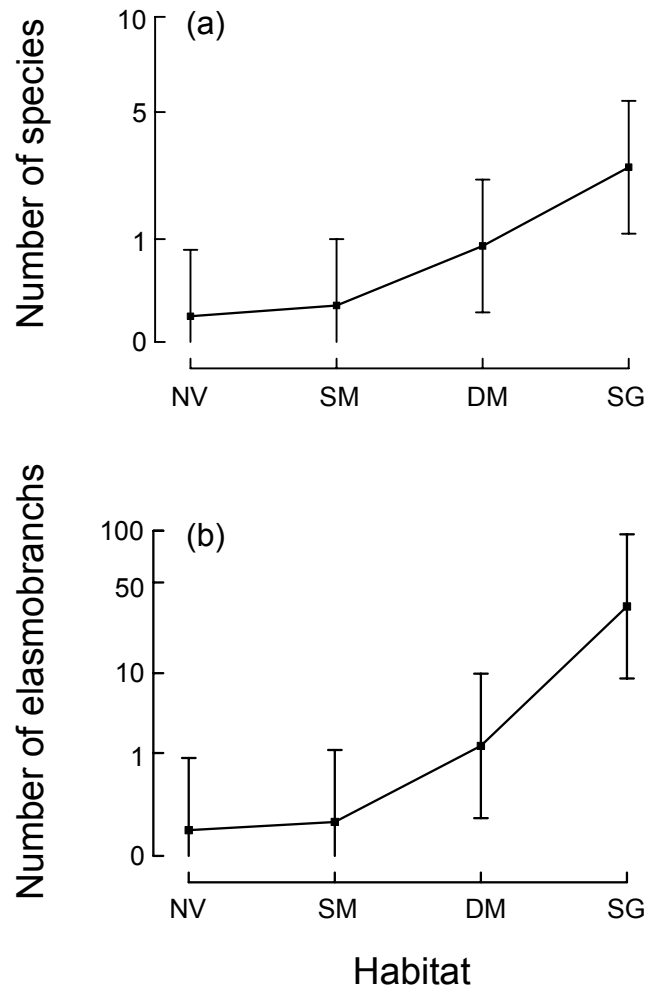
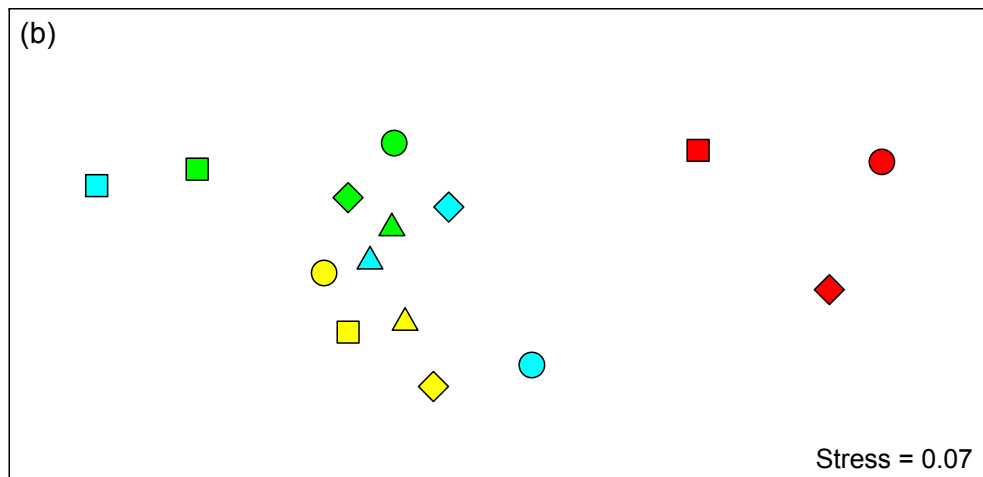
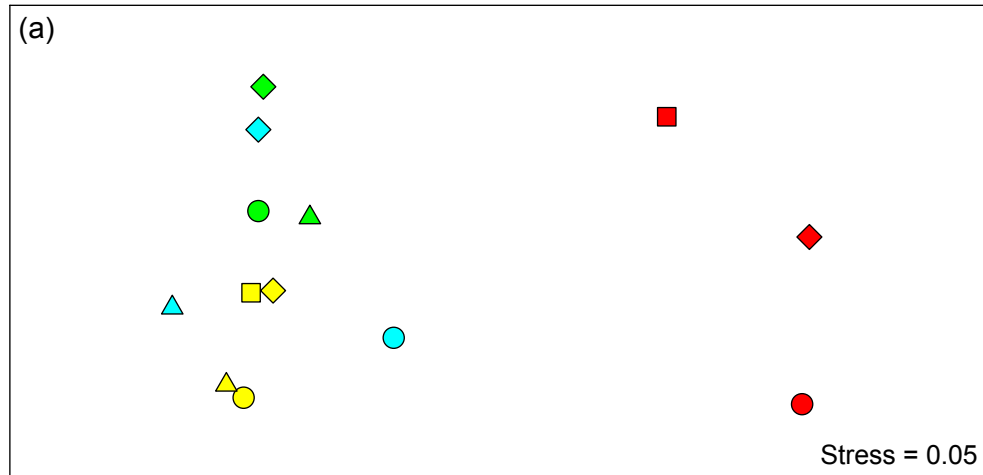


Figure 3.6 Mean \pm 95% confidence limits for (a) number of elasmobranch species and (b) number of elasmobranchs in four habitat types. NV, no vegetation nearby; SM, sparse mangroves; DM, dense mangroves; SG, seagrass.

3.3.5 Ordination of gillnet catches

MDS ordination of the mean numbers of the various elasmobranch species in each season resulted in the points for the samples for the three unvegetated sites in each season forming a group that lay in the left of the ordination plot and well separated from those for seagrass in the right of the plot (Fig. 3.7a). Within the group of samples for the unvegetated sites, those for the site near dense mangroves formed a tight and discrete group that lay in the lower part of the plot and directly below the tight group of samples representing the site near sparse mangroves. Two of the samples from the site with no vegetation in the vicinity lay to either side of those from the unvegetated site that contained dense mangroves nearby, whereas the third lay amongst those for the site with sparse mangroves nearby (Fig. 3.7a). The samples from seagrass and the site with no vegetation nearby were more widely dispersed than those in the unvegetated sites near dense and sparse mangroves, which is reflected in the much higher dispersion values of 1.5 and 1.6, respectively, vs 0.56 and 0.79, respectively. In each of the three unvegetated sites, the samples for spring, and also for winter at the site near dense mangroves, lay above those for autumn and summer.

ANOSIM showed that the species composition of the elasmobranchs differed significantly among the four sites ($P < 0.01$; R statistic = 0.556), but not among seasons ($P > 0.05$; R statistic = -0.108). Pairwise comparisons demonstrated that the composition of the samples from each site differed significantly from that of the samples at each other site, except in the cases of the site with no vegetation nearby vs the sites near both sparse and dense mangroves. The species designated by SIMPER as typifying both the site with no vegetation nearby and the site near sparse mangroves were *Carcharhinus cautus* and *Negaprion acutidens*, whereas *C. cautus* and *Rhinobatus typus* typified the site near dense mangroves and *Hemigaleus microstoma*, *Chiloscyllium punctatum* and *Rhizoprionodon*



Site	No vegetation nearby	Unvegetated Near sparse mangroves	Near dense mangroves	Vegetated Seagrass
Summer	▲	▲	▲	
Autumn	●	●	●	●
Winter	■	■	■	■
Spring	◆	◆	◆	◆

Figure 3.7 Non-metric multidimensional scaling ordination of (a) mean numbers of the various elasmobranch species and (b) mean numbers of the various elasmobranch and teleost species collectively that were caught by gillnetting in each season at each site in Herald Bight. Note that seagrass was not sampled in summer (see Materials and Methods for rationale) and that no elasmobranchs were caught in winter in either the unvegetated site that had no vegetation nearby or the one that was located near sparse mangroves.

acutus typified the seagrass site.

The mean numbers of the various teleost species were next included with those for elasmobranchs, thus providing samples containing fish in winter for the unvegetated sites both with no vegetation nearby and with sparse mangroves in the vicinity, and then subjected to MDS ordination. The samples from over seagrass and near both dense and sparse mangroves each still formed discrete groups in similar relative locations on the ordination plot (Fig. 3.7b). The samples from the site with no vegetation present nearby lay either to the left, between or to the right of those for the two sites near mangroves and were more widely dispersed than those from the two sites near mangroves, which is reflected in MVDISP values of 1.44 vs 0.65 and 0.80, respectively. A one-way ANOSIM showed that, overall, the compositions of elasmobranchs and teleosts collectively differed significantly between sites ($P < 0.05$; R statistic = 0.456), but not among seasons ($P > 0.05$; R statistic = -0.025). Pairwise comparisons showed that the compositions at each site were significantly different from each other site ($P < 0.05$), except in the cases of the site with no vegetation present nearby vs the sites near both sparse and dense mangroves ($P > 0.05$). The species designated by SIMPER as typifying the site with no vegetation nearby and the site near sparse mangroves were *Carcharhinus cautus* and *Pomatomus saltatrix*, whereas *Mugil cephalus* and *Pomatomus saltatrix* typified the site near dense mangroves and *Hemigaleus microstoma*, *Chiloscyllium punctatum* and *Rhizoprionodon acutus* typified the seagrass site.

3.4 Discussion

3.4.1 Use of Herald Bight as a nursery area by elasmobranchs

The presence of an umbilical scar on juveniles of seven of the ten shark species caught in Herald Bight, which indicates that these juveniles had been recently born, demonstrates that the shallow waters of this bay act as a nursery area for these species. Since *Carcharhinus*

cautus gives birth in November in Shark Bay (Chapter 5), and several of the juveniles of this species bore umbilical scars in December and January, such scars frequently last on this species for about two months. The presence of an umbilical scar on one juvenile in both March and April is possibly the result of a slightly extended pupping season. The period during which umbilical scars were found on *Negaprion acutidens* was the same as with *C. cautus*, and thus this species presumably gives birth at a similar time to *C. cautus* and uses the same waters as a nursery area during the same months. The months during which umbilical scars were present on other species, for which there are no reproductive data, were restricted, e.g. July for *Carcharhinus brevipinna*, November and January for *Carcharhinus limbatus* and April and July for *Rhizoprionodon acutus*.

Although the majority of the juveniles of *N. acutidens*, which ranged in length from 630 to 1510 mm, were immature, i.e. no yolked oocytes present in right ovary and both uteri flaccid and not yet enlarged, the two largest individuals were maturing, i.e. yolked oocytes were present in the right ovary and both uteri were becoming enlarged. Thus, some of the juveniles of this species appear to remain in the shallow, nearshore waters of Herald Bight until they begin maturing, when they possibly emigrate from the nearshore, shallow waters of this bay. Since all of the *R. acutus* that were caught were immature and only one had attained the length at which this species becomes mature, i.e. 700–800 mm for females and 680–720 mm for males (Bass *et al.*, 1975; Stevens & McLoughlin, 1991), the juveniles of this species also apparently remain within the nearshore, shallow waters of the bay until they start to mature. This parallels the situation in Cleveland Bay in north-eastern Australia, where none of the individuals of this species caught exceeded 720 mm in length (Simpfendorfer & Milward 1993). Although only a few recently-born individuals of *R. acutus* were caught, large numbers of the small individuals of this species, which are slender and thus not particularly susceptible to meshing in my gillnet, were observed in the

shallow tidal lagoons that form at high tide during the summer. Ten of the twelve *C. brevipinna* caught were recently born and the other two were only slightly longer than those recently-born individuals. Thus, this species uses the nearshore, shallow waters of Herald Bight as a primary nursery area *sensu* Bass (1978) and subsequently moves to a secondary nursery for the rest of its juvenile life. Since *C. brevipinna* is a widely distributed species that moves over large distances, nurseries for this species are probably very widespread.

The role of the nearshore waters of Herald Bight as a nursery area for sharks is also highlighted by the far larger number of sharks caught by the panel with the smallest mesh in the gillnet than that caught by the two panels with larger meshes, which both retained fish of a significantly greater length than the smallest mesh. Furthermore, the mean lengths of fish caught in the two largest mesh sizes were not significantly different suggesting that larger sharks were not available to be caught by the largest mesh size. Such a conclusion is consistent with the fact that Kirkwood & Walker (1986) demonstrated that the mean lengths of the gummy shark *Mustelus antarcticus* caught in eight different meshes of their gillnets increased progressively with increasing mesh size.

The specific nursery role of the nearshore, shallow waters of Herald Bight for species such as *C. brevipinna*, *N. acutidens* and *R. acutus* is consistent with all individuals of these species being immature. For example, the maximum lengths of *C. brevipinna* and *N. acutidens* in the gillnet samples were only 810 and 1510 mm, respectively, whereas the maximum recorded lengths for these species are 2800 and 3000 mm, respectively (Last & Stevens, 1994). In contrast, *C. acutus* was represented in the samples by recently-born juveniles, juveniles without umbilical scars and adults, and thus by all post-partum stages and close to the full length range of this species (Last & Stevens, 1994). Thus, this species can spend the whole of its life in nearshore waters in Shark Bay, paralleling the situation in

northern Australia (Lyle, 1987). The single *Carcharhinus plumbeus* caught in the nearshore, shallow waters of Herald Bight in July was a pregnant female, whose large mass accounts for this species ranking third among sharks in terms of biomass, even though only four individuals of this shark were collected.

Although only a small number of juvenile *Rhinobatus typus* were caught by gillnetting at the nearshore sites of Herald Bight, the use of other sampling methods, *i.e.* seine netting, spearing and rod and line angling, demonstrated that this species is abundant in the unvegetated region of Herald Bight (Chapter 2). The low numbers of *R. typus* caught in the gillnet reflects a combination of their slow-moving and bottom-dwelling life and a triangular disc shape which reduces their susceptibility to meshing in gillnets.

3.4.2 *Partitioning of habitats by elasmobranchs*

The use of MDS ordination demonstrated very clearly that the composition of the elasmobranch fauna in seagrass meadows was very different from that in each of the three unvegetated habitats. This difference reflected that *R. acutus*, *C. brevipinna* and *C. punctatum* were caught very largely or exclusively over seagrass, whereas most of the large numbers of *C. cautus* and all of the *N. acutidens* came from the three unvegetated habitats. The particular importance of the meadows of *Posidonia australis* as a nursery area for elasmobranchs is emphasised by the fact that the number of elasmobranch species and number of elasmobranchs in seagrass were both significantly greater than at the unvegetated site where no vegetation was present nearby and, in the case of the latter variable, also where sparse mangroves were present in the vicinity. The dense vertical foliage of *P. australis* prevents its utilisation by large predatory fish (Travers & Potter 2002) and thus reduces the likelihood of predation on these elasmobranchs. The seagrass

also contains an abundance of the small portunids and certain seagrass-dwelling teleosts on which *R. acutus* feeds (Chapter 4).

Although the compositions of the elasmobranch fauna in the unvegetated sites near sparse and dense mangroves were significantly different, neither of them differed significantly from that at the unvegetated site where no vegetation was present nearby. Furthermore, the points on the ordination plot for the samples from the former two sites were much more tightly grouped, and remained so even when teleosts were included in the ordination, indicating that, as a whole, the ichthyofaunal composition at these two sites remains more discrete and changes less throughout the year.

It is also relevant that the number of species at the two unvegetated sites where mangroves were present nearby were both significantly greater than at the unvegetated site where no vegetation was present nearby. Since the gillnet would have caught fish moving in and out of the mangroves at high tide, this finding suggests that the mangroves provide an important habitat for elasmobranchs at around the time of high tide. It is also relevant that the densities of elasmobranchs were far greater at the site near dense mangroves than at the unvegetated site where no vegetation was present nearby. This implies that the dense mangroves constitute particularly important habitats for elasmobranchs. Such a view is entirely consistent with visual observations that, at around high tide, elasmobranchs enter the dense mangroves, including those in the inlet located near to where the gillnet was set (see Fig. 2.1 in Chapter 2).

3.4.3 *Seasonal changes*

Since the number of species and number of elasmobranchs in the nearshore waters of Herald Bight were significantly greater in summer and autumn than in winter, and also than

in spring in the case of the former variable, elasmobranchs, in general, tended to move into these shallow waters when temperatures were greatest.

Although a one-way ANOSIM failed to detect an overall significant seasonal difference in the composition of the elasmobranch fauna caught in Herald Bight, this is hardly surprising in view of the overwhelming influence of habitat type on species composition. The latter feature is emphasised by the fact that the points on the ordination plot for the samples for any given season in each of those habitat types lay far closer to those of other seasons at that habitat type than to that of the same season in another habitat type. However, the points for spring in each of the three unvegetated habitats, and also for winter in the site near dense mangroves where elasmobranchs were caught in that season, lay above those for autumn and summer. Furthermore, the points for the winter and spring samples also lay above that for autumn at the seagrass site. These data strongly indicate that the species composition in each habitat type underwent a small but similar pattern of seasonal change. However, the MVDISP values demonstrate that seasonal differences were more pronounced in seagrass and in the unvegetated site that contained no seagrass nearby than at the two sites near mangroves.

The indication that the composition of the elasmobranch fauna in Herald Bight undergoes seasonal changes is consistent with the trends exhibited by the numbers of elasmobranchs caught in the different months (see Table 3.2). Thus, for example, although *C. cautilus* was more abundant between late spring and mid-autumn than between early winter and mid-spring, *R. acutus* was most abundant in mid-autumn and mid-winter and *N. acutidens* was caught mainly in summer and autumn. Furthermore, the other less numerous species were often not caught in the same months. Thus, the composition of the elasmobranch fauna in Herald Bight clearly does not remain constant throughout the year. However, it is worth noting that, although the points for the samples for all fish in the two

unvegetated sites near mangroves and the seagrass site each still grouped tightly together on the ordination plot, *i.e.* when teleosts and elasmobranchs were analysed collectively, the samples for the different seasons were no longer arranged in a similar pattern within each habitat type.

In summary, this study provides the first data on the number of species and abundance of elasmobranchs and the composition of the elasmobranch fauna of the World Heritage Area of Shark Bay and how these variables are influenced in this type of embayment by habitat type and season. It also apparently represents the first study to determine statistically whether the species composition of the elasmobranch assemblages in different habitats within a water body differ and, if so, then to elucidate statistically which species contributed most to any such differences. The results of this study, together with that on the dietary compositions of the most abundant species (Chapter 4), demonstrate that the spatial and food resources in Herald Bight are partitioned among the various elasmobranch species found in these waters. This reduces the potential for competition for these resources in these waters.

CHAPTER 4

**Comparisons between the diets of four abundant species of elasmobranch
in a subtropical embayment. Implications for resource partitioning**

4.1 Introduction

Since elasmobranchs are frequently apex predators in marine ecosystems, information on their dietary compositions is essential for understanding trophic relationships in these systems (Cortes, 1999). The crucial role played by sharks in food webs is well illustrated in northern Australia, for example, where a substantial component of the natural mortality of commercial penaeids is attributable to predation by these elasmobranchs (Blaber *et al.*, 1990; Brewer *et al.*, 1991). Although there is a considerable amount of data on the contributions made by different prey types to the diets of a single species or group of species of elasmobranch (*e.g.* Babel, 1967; Ebert *et al.*, 1991; Salini *et al.*, 1991; Stevens & McLoughlin, 1991; Ellis *et al.*, 1996; Simpfendorfer *et al.*, 2001a, b), there is a paucity of data on the extents to which the diets of the elasmobranch species found in a region vary with habitat, time of year and body size. Indeed, work on the prey of four species of urolophid rays on the lower west coast of Australia represents one of the few attempts to subject quantitative data on the dietary composition of co-occurring elasmobranchs to analyses that enable the influence of these three variables to be explored statistically (Platell *et al.*, 1998). That study demonstrated that the dietary compositions of each urolophid species changed with body size and sometimes differed among sites and seasons, presumably reflecting spatial and temporal differences in the types of prey available.

Shark Bay houses a commercial fishery for two penaeid species and a single species of portunid crab (Kailola *et al.*, 1993) and contains the most extensive and diverse seagrass meadows in the world (Walker, 1989). Recent work has emphasised that the dietary compositions of certain teleost species in Shark Bay are influenced markedly by whether these species are found in seagrass or over bare sand, reflecting differences in the suite of prey present in these two habitat types (Linke *et al.*, 2001). Preliminary sampling of the nearshore waters in a bay (Herald Bight) within Shark Bay showed that the giant

shovelnose ray *Rhinobatus typus*, the nervous shark *Carcharhinus cautus* and the lemon shark *Negaprion acutidens* typically occupy unvegetated areas in Herald Bight, whereas the milk shark *Rhizoprionodon acutus* normally lives in nearby areas that contain seagrass meadows (*Posidonia australis*). This bay acts as a nursery area for the juveniles of each of these species and as a habitat for *C. cautus* throughout the whole of its life (see Chapter 3).

The aim of the present study was to test the following hypotheses. 1) Food resources within the confines of Herald Bight will be partitioned among the above single species of rhinobatid ray and three species of carcharhinid shark that are each abundant in that bay. 2) The marked differences between the benthic and pelagic habit, mode of feeding and mouth morphology of rhinobatid rays and carcharhinid sharks will be reflected in particularly marked differences in the dietary compositions of the species representing these two groups of elasmobranch. 3) Since *R. acutus* is the only one of the three shark species that is typically found over seagrass, its dietary composition will be the most distinct of those species. 4) The size and type of prey of each species will change with increasing body size. 5) Penaeid and portunid crustaceans, which are very abundant in Shark Bay, will constitute important components of one or more of the elasmobranch species. 6) The composition of the prey ingested will change during the year.

4.2 Materials and methods

4.2.1 Sampling locations and regime

Details of the sampling regime and gear used to catch elasmobranchs in Herald Bight are provided in Chapter 2. The numbers of individuals of each of the four most abundant species, *i.e.* *R. typus*, *C. cautus*, *N. acutidens* and *Rhizoprionodon acutus*, from which the stomachs were removed and frozen for subsequent analyses of their contents, were 316, 219, 59 and 41, respectively.

4.2.2 *Dietary analyses*

The degree of fullness of those stomachs that contained food was visually estimated on a scale of 1 to 10 and the contents of each of those stomachs removed. Each dietary item was identified to the lowest possible taxon, using a dissecting microscope whenever necessary. The penaeid species were identified using Chan (1998). The items in the stomach contents were allocated to one of 30 dietary categories or, for the following reasons, to one of four further groups. Since unidentifiable crustaceans, teleosts and other material are likely to contain the remnants of more than one dietary category and could thus bias the results of analyses, none of these three components was included as a dietary category in the multivariate analyses of dietary compositions. Furthermore, sediment, which comprised predominantly inorganic material and whose contributions to the stomach contents of each species are likewise shown in Table 4.1, is also not considered a *bona fide* dietary category. The frequency with which the various dietary categories and other components were found in the stomach contents of all individuals of each species (%F) was calculated. The percentage contributions made to the stomach contents of each individual by the numbers of each dietary category (%N) and by the volumes of each dietary category and each of the other components (%V) were calculated. Note that the volume of each dietary category and the other components were expressed using the points method, which incorporates the values for stomach fullness (see Hynes, 1950; Hyslop, 1980). Volumetric rather than numerical data have been used to analyse dietary compositions, since they represent better the relative importance of each dietary category and overcome the problems that digestion can pose for enumerating prey items (Hyslop, 1980). Since a preliminary examination showed that the dietary compositions of the females and males of each of the four species were very similar, the volumetric data for the stomach contents of the two sexes of each species were pooled.

Table 4.1 Frequency (%F) with which the 30 dietary categories and other components occurred in the stomachs of *Rhinobatus typus*, *Carcharhinus cautus*, *Rhizoprionodon acutus* and *Negaprion acutidens* and, where applicable, each of their percentage contributions to the overall number (%N) and volume (%V) of those categories and components in the stomach contents of each of these elasmobranchs.

Major taxa and dietary categories	<i>Rhinobatus typus</i>			<i>Carcharhinus cautus</i>			<i>Rhizoprionodon acutus</i>			<i>Negaprion acutidens</i>		
	%F	%N	%V	%F	%N	%V	%F	%N	%V	%F	%N	%V
Mollusca	1.5	0.6	0.3	25.4	19.5	15.0	21.4	20.7	17.9	10.0	5.3	2.6
Bivalvia	0.7	<0.1	<0.1	1.7	3.2	0.4						
Gastropoda	0.4	<0.1	<0.1	3.4	2.2	2.6						
Cephalopoda	0.4	0.5	0.2	20.3	14.1	12.0	21.4	20.7	17.9	10.0	5.3	2.6
Crustacea	100	98.9	96.4	14.4	10.8	9.9	10.7	10.3	10.9	5.0	2.6	2.6
Diogenidae	1.1	0.2	0.4									
Grapsidae	0.7	<0.1	<0.1	1.7	1.6	0.2						
Mysidacea	1.5	3.2	0.8									
Ocypodidae	0.4	<0.1	<0.1									
Penaeidae	92.9	83.8	70.6	1.7	1.1	0.2	3.6	3.4	0.6			
Portunidae	54.5	11.7	22.5	10.2	7.6	9.4	7.1	6.9	10.3	5.0	2.6	2.6
Stomatopoda	0.4	<0.1	<0.1									
Unidentifiable	4.9	1.0	2.1	0.8	0.5	0.1						
Elasmobranchii										15.0	13.2	11.5
Rhinobatidae										15.0	13.2	11.5
Teleostei	4.8	0.4	2.1	82.2	68.6	68.2	63.3	69.0	67.4	100	78.9	83.3
Atherinidae	0.4	<0.1	0.3	5.1	3.2	2.6	14.2	13.8	16.8	15.0	10.5	13.5
Belonidae				1.7	2.1	2.3				5.0	2.6	4.5
Centropomidae							3.6	3.4	4.6			
Clupeidae							3.6	3.4	5.2	5.0	21.1	5.1
Gobiidae				0.9	0.5	<0.1						
Harpodontidae				0.9	0.5	1.2						
Labridae				3.4	2.7	2.7	3.6	3.4	3.4	5.0	2.6	1.3
Lethrinidae				0.8	0.5	0.9						
Monacanthidae				2.5	2.2	0.9						
Mugilidae				0.8	0.5	0.9						
Muraenidae				0.9	0.6	0.9						
Platycephalidae	0.4	<0.1	<0.1	2.5	1.6	3.4						
Pseudochromidae				0.9	0.5	0.4						
Sillaginidae	0.4	<0.1	0.4	5.9	3.8	5.6	3.6	3.4	5.7	10.0	5.3	10.3
Sparidae				0.8	0.5	0.5				5.0	2.6	6.4
Sygnathidae	0.4	<0.1	<0.1	0.8	0.5	0.1				5.0	2.6	2.6
Terapontidae				3.4	3.8	4.6	3.6	3.4	1.1			
Unidentifiable	3.4	0.3	1.3	50.9	44.8	41.2	31.1	37.9	30.6	55.0	31.6	39.8
Reptilia				1.1	1.1	1.7						
Lepidosauria				1.1	1.1	1.7						
Macrophyta	1.5		<0.1	24.6		2.4	3.6		0.4			
Seagrass	1.5		<0.1	24.6		2.4	3.6		0.4			
Other	1.9		0.5	6.0		1.5	17.9		3.4			
Sediment				0.9		<0.1						
Unidentifiable matter	1.9		0.5	5.1		1.5	17.9		3.4			
Number of fish		316			219			59			41	
Stomachs with food		268			118			28			20	

The mean percentage volumetric contributions of the various dietary categories to the diets of successive length classes, *i.e.* ≤ 590 , 600–890, 900–1190 and ≥ 1200 mm, of each of the four species in the different seasons, which are each referred to as a dietary sample, were subjected to non-metric multidimensional scaling (MDS) ordination, to determine whether species, body size or season exerted the greatest overall influence on the dietary compositions of these elasmobranchs. Since species was shown to be the most important of these three factors (see Results), the question of whether the dietary composition of those species, for which there were sufficient data, was influenced by body size and/or season was then examined. Because most of the different size classes were represented in each season only in the case of *R. typus*, the dietary data for each size class of each species in all seasons were pooled to facilitate comparisons among the diets of corresponding size classes of the different species. For this purpose, the mean percentage volumetric contributions made to the diets of each species by eleven dietary groups, that each comprise one or a group of taxonomically-related dietary categories, were calculated and plotted in the form of histograms. This enabled rapid visual examination of how the most important sources of the food of these species changes with increasing body size. The mean volumetric contributions of the various dietary categories of each size class of each species were then subjected to ordination to ascertain whether there was evidence that the dietary compositions of each species underwent progressive changes as a species increased in size.

The question of whether dietary composition was influenced by season was explored in *R. typus* and *C. cautus*, the two species for which there were substantial dietary data for each season. However, an examination of the dietary data showed that the stomachs of individual fish often contained only a few of the large number of dietary categories recognised in this study, *i.e.* 30. This is a common problem with dietary studies

of the current type and has been overcome in other studies by pooling dietary data for groups of individuals (Linke *et al.*, 2001; Platell & Potter, 2001; Schafer *et al.*, 2002). Thus, the dietary data for individuals of both *R. typus* and the less abundant *C. cautilus* in each season were randomly allocated into groups of five and three, respectively, and a mean for each of the resulting groups calculated. The numbers of such groups (= dietary samples) in each season were sufficient for analysis by MDS ordination and associated statistical tests to ascertain whether the dietary compositions of these species changed during the year. A comparable approach involved the pooling and meaning of the volumetric dietary data for groups of five individuals within each size class of the most abundant species, *i.e.* *R. typus*. This also enabled MDS ordination and associated tests to be used to explore whether the dietary composition of this batoid changed with increasing body size.

Prior to subjecting the mean volumetric contributions of the dietary categories in each dietary sample to MDS ordination, they were square root transformed and a similarity matrix constructed using the Bray-Curtis similarity coefficient. The matrix was then ordinated using the multidimensional scaling techniques described in the PRIMER v5.2.2 package (Clarke & Gorley, 2001). One-way Analyses of Similarities (ANOSIM) were employed to test whether dietary compositions differed significantly amongst the four species and among seasons for *R. typus* and *C. cautilus* and among the size classes of *R. typus*. Where applicable, Multivariate Dispersion (MVDISP) was used to determine the degree of dispersion of the dietary samples on ordination plots (Sommerfield & Clarke, 1997) and Similarity Percentages (SIMPER) was employed to determine the dietary categories that typified particular groups and/or contributed most to the dissimilarities between groups (Clarke, 1993).

The species diversity in the diet, which corresponds to dietary breadth (Marshall & Elliot, 1997), was calculated for the different length classes of each of the four species using the Shannon-Wiener index (Pielou, 1966).

4.3 Results

4.3.1 Ranking and contributions of dietary components

The percentage number of stomachs that contained food was far greater in the case of the ray *Rhinobatus typus* (84.8%) than the sharks *Carcharhinus cautus* (53.9%), *Rhizoprionodon acutus* (47.5%) and *Negaprion acutidens* (48.8%). On the basis solely of stomachs containing food, the mean stomach fullness of each species ranged from 6.2 in *R. acutus* to 7.9 in *N. acutidens*. The total number of dietary categories recorded in the stomachs of each species ranged from 10 in both *R. acutus* and *N. acutidens* to 15 in *R. typus* and 23 in *C. cautus* (Table 4.1).

The values given in the following account of the dietary data refer specifically to those for elasmobranchs with stomachs containing food. Crustaceans were found in the stomachs of all *R. typus* and made the greatest contribution to the total numbers and volumes of all dietary categories in this species, *i.e.* 98.9 and 96.4%, respectively (Table 4.1). Although at least 12 crustacean species were recorded in the stomachs of *R. typus*, two penaeid species (*Penaeus merguensis* and *Melicertus latisulcatus*) and a single portunid species (*Portunus pelagicus*) collectively contributed 93.1% to the total volume of the dietary categories of this ray. In contrast, crustaceans (mainly *Portunus pelagicus*) were present in only 14.4, 10.7 and 5.0% of the stomachs of *C. cautus*, *R. acutus* and *N. acutidens*, respectively, and made only minor numerical and volumetric contributions to the stomach contents of these shark species (Table 4.1).

Teleosts were found in only 4.8% of the stomachs of *R. typus* and contributed only 2.1% to the total volume of their stomach contents. However, they were the most important dietary taxa for the other three species (Table 4.1). Thus, teleosts were present in 82.2, 63.3 and 100% of the stomachs of *C. cautus*, *R. acutus* and *N. acutidens*, respectively, and contributed 68.2, 67.4 and 83.3% to the total dietary volume of these species, respectively. The teleosts that, in terms of volume, contributed most to the dietary composition of *C. cautus* were sillaginids, terapontids, platycephalids and labrids, whereas atherinids were the most important contributor to the diet of both *R. acutus* and *N. acutidens*. Individuals of *R. typus* were ingested by 15% of the individuals of *N. acutidens* (Table 4.1).

Although cephalopods were present in very few stomachs of *R. typus*, they were found in 10.0 to 21.4% of those of the three shark species and contributed between 2.6 and 17.9% to the dietary volume of these species (Table 4.1). Bivalves and gastropods were recorded only in low numbers and volumes in the stomach contents of *R. typus* and *C. cautus* and were not found in the stomachs of *R. acutus* and *N. acutidens*. Lepidosaurids comprised 1.7% of the total volume of the stomach contents of *C. cautus* and were not found in those of any of the other three species (Table 4.1).

4.3.2 Comparisons of dietary compositions

Following ordination of the volumetric dietary data for the different size classes of each species in the four seasons, the dietary samples of *R. typus* formed a particularly discrete group on the left side of the plot, whereas those for *C. cautus* produced a relatively tight group in the centre of that plot (Fig. 4.1a). The dietary samples of *R. acutus* were distributed across the upper half of the plot, whereas all but one of those of *N. acutidens* occupied the right half of the plot (Fig. 4.1a). The samples of *R. typus* were far less scattered than those for the three shark species, a feature reflected in much lower dispersion

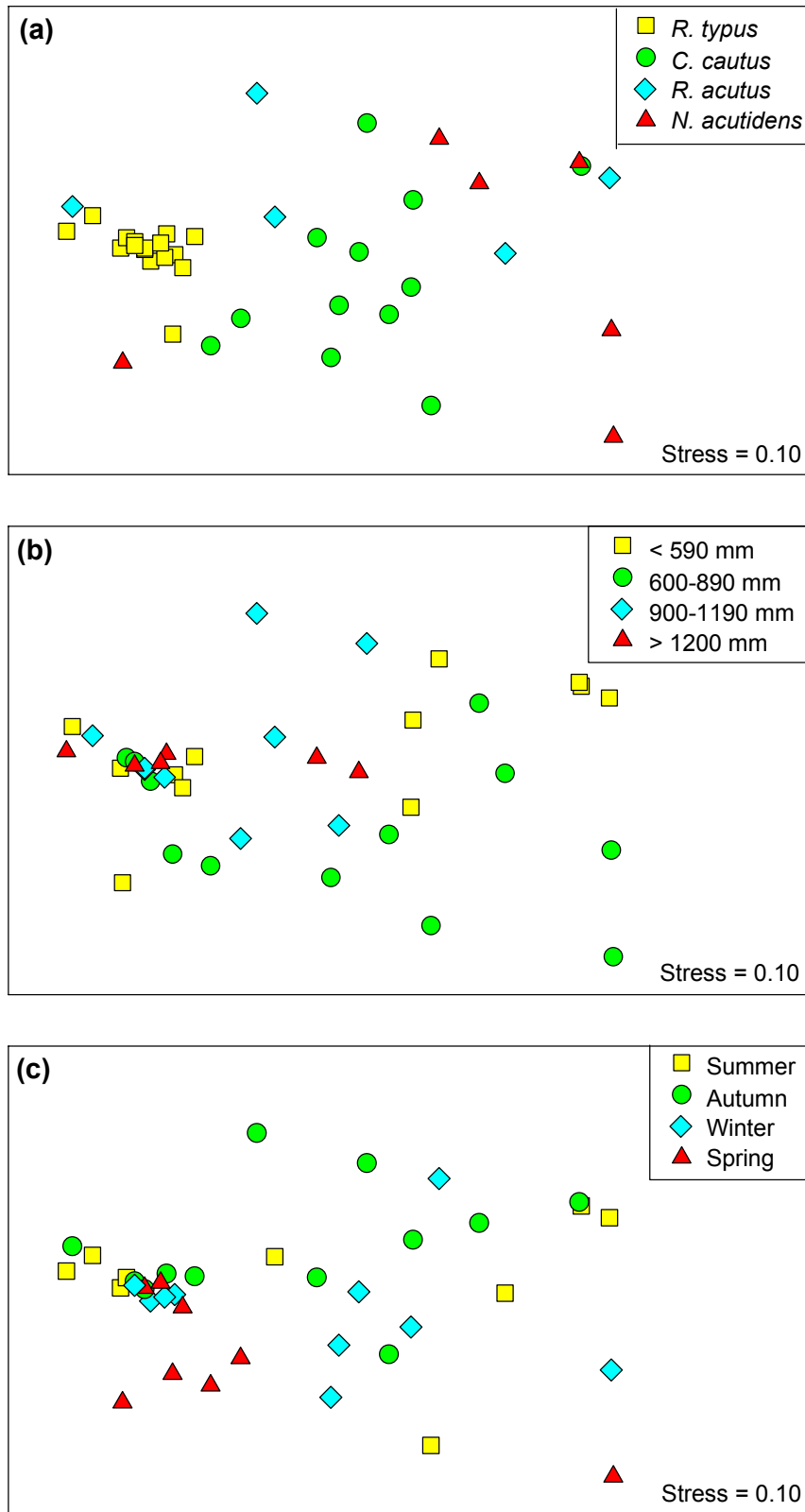


Figure 4.1 Non-metric multidimensional scaling ordination of the mean percentage volumetric contributions of the various dietary categories to the diets of each species, coded for (a) species, (b) body size and (c) season.

values, *i.e.* 0.59 vs 1.48–1.77. ANOSIM demonstrated that the dietary compositions of the four species were significantly different overall ($P < 0.001$; R statistic = 0.605), and also for each of the pairwise comparisons except for *N. acutidens* vs *R. acutus* ($P > 0.05$). In the case of pairwise comparisons between species, the R statistic values were greatest between *R. typus* and the three shark species (0.703–0.893; $P < 0.001$) and least for *C. cautus* vs both *N. acutidens* and *R. acutus* (R statistic = *ca* 0.235; $P < 0.05$). The dietary category designated by SIMPER as most responsible for differences between the dietary compositions of *R. typus* and the three shark species was the Penaeidae, whereas *C. cautus* ingested relatively greater amounts of the Portunidae than either of the two remaining shark species, for which the Atherinidae was more important.

The dietary samples showed no tendency to form any tight or discrete groupings when they were coded for either length class (Fig. 4.1b) or season (Fig. 4.1c). Furthermore, ANOSIM showed that the overall dietary compositions of neither individual length classes nor different seasons differed significantly ($P > 0.05$).

4.3.3 *Size-related changes in dietary compositions and dietary breadths*

The diet of each length class of *R. typus* consisted almost exclusively of penaeid prawns and portunid crabs, with the percentage contributions made by the former declining from as high as 85.6% in the smallest fish to 55.3% in the largest fish, whereas that of the latter group increased from 9.8 to 41.9% (Fig. 4.2). Although teleosts were the dominant prey in the diets of all length classes of *C. cautus*, their volumetric contribution to the diet declined progressively from 97.1% in the smallest fish to 48.8% in the largest fish. The other major contributors to the diet of this shark species were cephalopods and portunid crabs in the case of fish between 600 and 1190 mm and portunids and reptiles with the largest fish (Fig. 4.2).

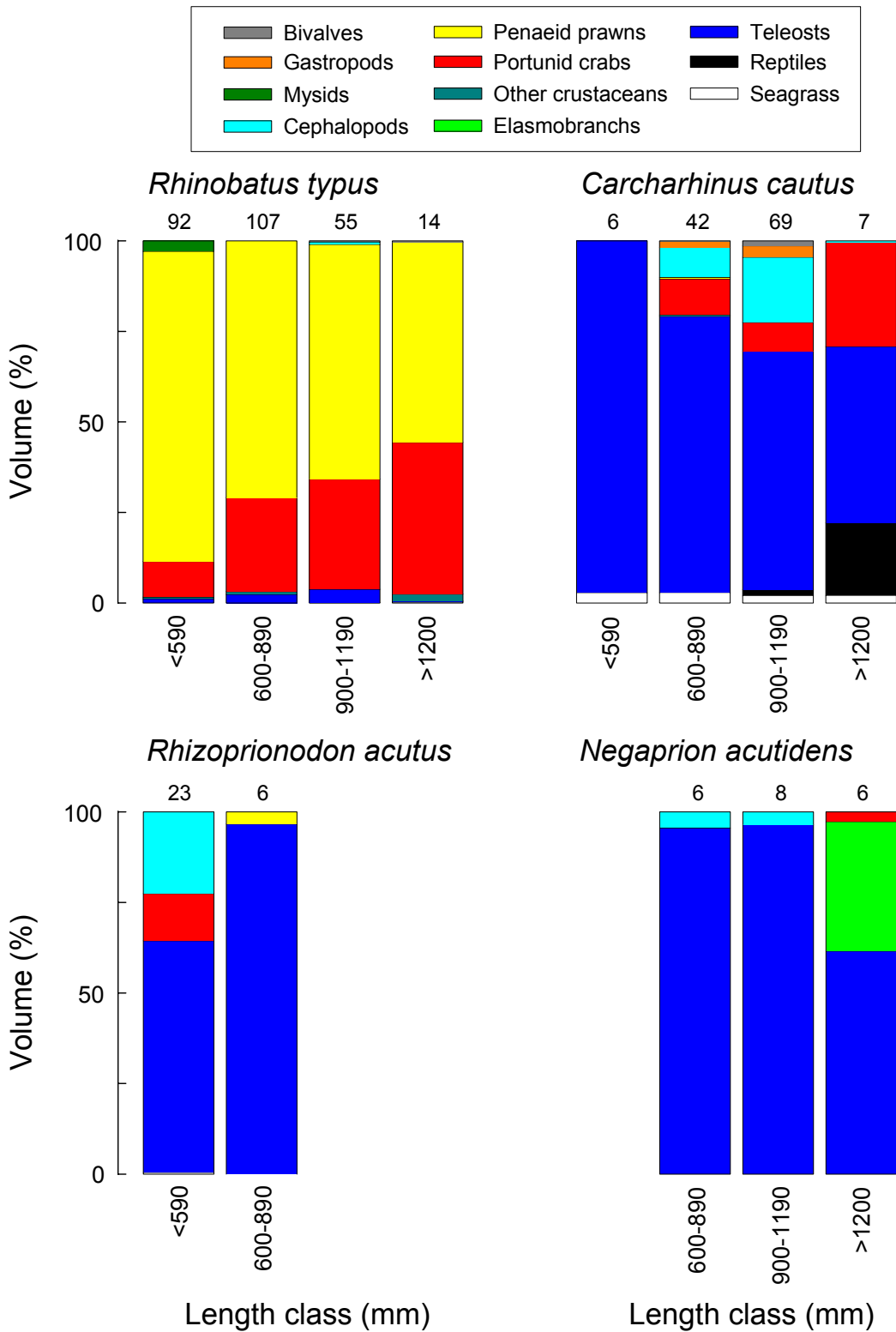


Figure 4.2 Mean percentage volumetric contributions of the different broad prey groups to the diets of sequential length classes of *Rhinobatus typus*, *Carcharhinus cautus*, *Rhizoprionodon acutus* and *Negaprion acutidens*. Sample sizes are given above the bars for each length class.

Although teleosts dominated the diets of both size classes of *R. acutus*, cephalopods and portunid crabs collectively contributed 36.6% to the diets of the smaller individuals of this species (Fig. 4.2). Teleosts were almost the only prey found in the stomachs of *N. acutidens* <1200 mm and were the main prey of this species \geq 1200 mm (Fig. 4.2). Elasmobranchs (*R. typus*) contributed *ca* 35% to the total volume of the stomach contents of the largest *N. acutidens* (Fig. 4.2).

The dietary breadth of *R. typus* increased with increasing body size and, for each length class, was less than that of each of the three shark species (Table 4.2). The dietary breadths were high for the two length classes of *C. cautus* and the single length class of *R. acutus* that were each represented by substantial numbers in the samples, *i.e.* 0.92, 0.93 and 0.82, respectively.

Table 4.2 Overall dietary breadths for successive length classes of *Rhinobatus typus*, *Carcharhinus cautus*, *Rhizoprionodon acutus* and *Negaprion acutidens*. Numbers in parentheses refer to number of individuals in each length class.

Length class (mm)	<i>Rhinobatus typus</i>	<i>Carcharhinus cautus</i>	<i>Rhizoprionodon acutus</i>	<i>Negaprion acutidens</i>
\leq 590	0.26 (92)	0.56 (6)	0.82 (23)	-
600–890	0.42 (107)	0.92 (42)	0.64 (5)	0.45 (6)
900–1190	0.46 (55)	0.93 (69)	-	0.79 (8)
\geq 1200	0.52 (14)	0.54 (7)	-	0.57 (6)

Following ordination of the dietary samples of the different length classes of *R. typus*, which were represented by the stomach contents of one or more groups of five individuals, all but one of the samples for the smallest fish lay in or close to the left hand side of the plot, and largely to the left or below those for the two intermediate length classes, *i.e.* 600–890 and 900–1190 mm (Fig. 4.3). Two of the three samples for the largest

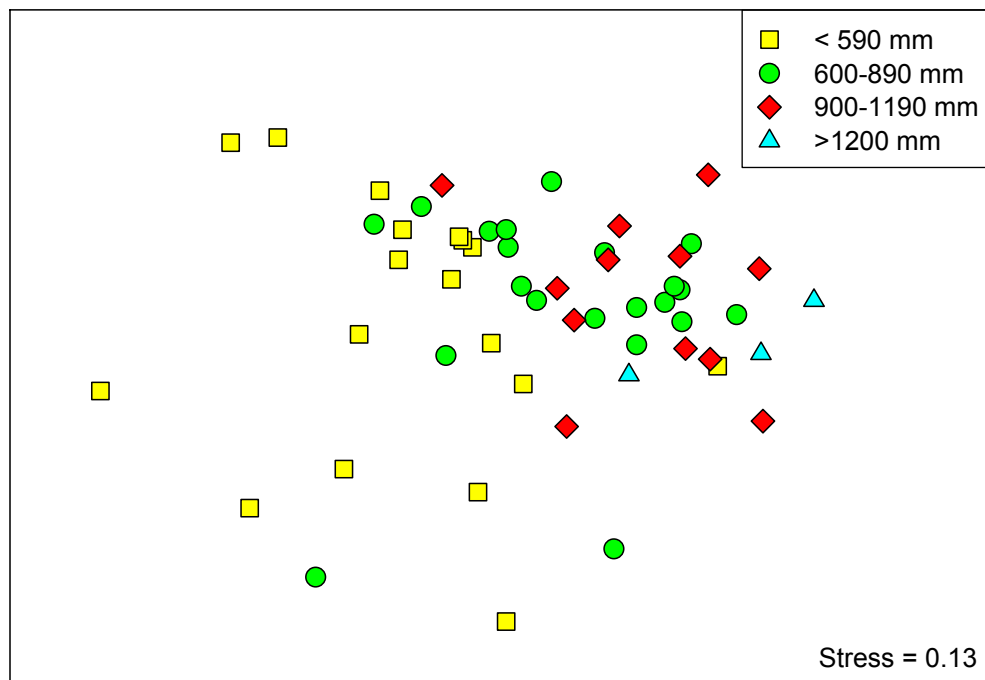


Figure 4.3 Non-metric multidimensional scaling ordination of the volumetric dietary data for sequential length classes of *Rhinobatus typus*, with each point (= dietary sample) representing meaned data for groups of five randomly-selected fish within each length class.

fish lay at the extreme right of the plot. ANOSIM showed that the dietary compositions of *R. typus* differed among size classes ($P < 0.001$, global R statistic = 0.189) and that the dietary composition of the < 590 mm length class differed significantly from that of each of the other three size classes, with R statistic values ranging from 0.222 ($P < 0.001$) for the ≤ 590 vs 600–890 mm size class to 0.459 ($P < 0.05$) for the ≤ 590 vs ≥ 1200 mm length classes.

Ordination of the volumetric dietary data for each length class of *R. typus*, *C. cautilus* and *N. acutidens* resulted, in the case of each species, in the dietary samples of the length classes comprising the smallest and largest fish lying on the left and right hand side of the plot, respectively (Fig. 4.4). This trend was particularly evident with *C. cautilus*, with the dietary samples for fish ≤ 590 mm lying on the far left of the plot and those for the ≥ 1200 mm length class situated on the far right of the plot and those for the 600–890 and 900–1190 mm length classes occupying the centre of the plot. Although the trends for *R. typus* were not as pronounced on the main plot that included all four species, dietary samples for that species clearly followed the same progressive change with increasing body size when the mean dietary data for each of its length classes were ordinated and plotted separately (Fig. 4.4).

4.3.4 Seasonal changes in the dietary compositions of *R. typus* and *C. cautilus*

Ordination of the volumetric dietary data for *R. typus* in the different seasons resulted in the dietary samples for winter and autumn each forming a narrow horizontal band just below the horizontal midline of the plot, whereas those for both summer and spring were scattered throughout the plot (Fig. 4.5a). The differences in the scatter of the samples are reflected in differences in the values for MVDISP, with those for winter and autumn, *i.e.* 0.50 and 0.75, respectively, being far less than those for summer and spring, *i.e.* 1.20 and 1.38,

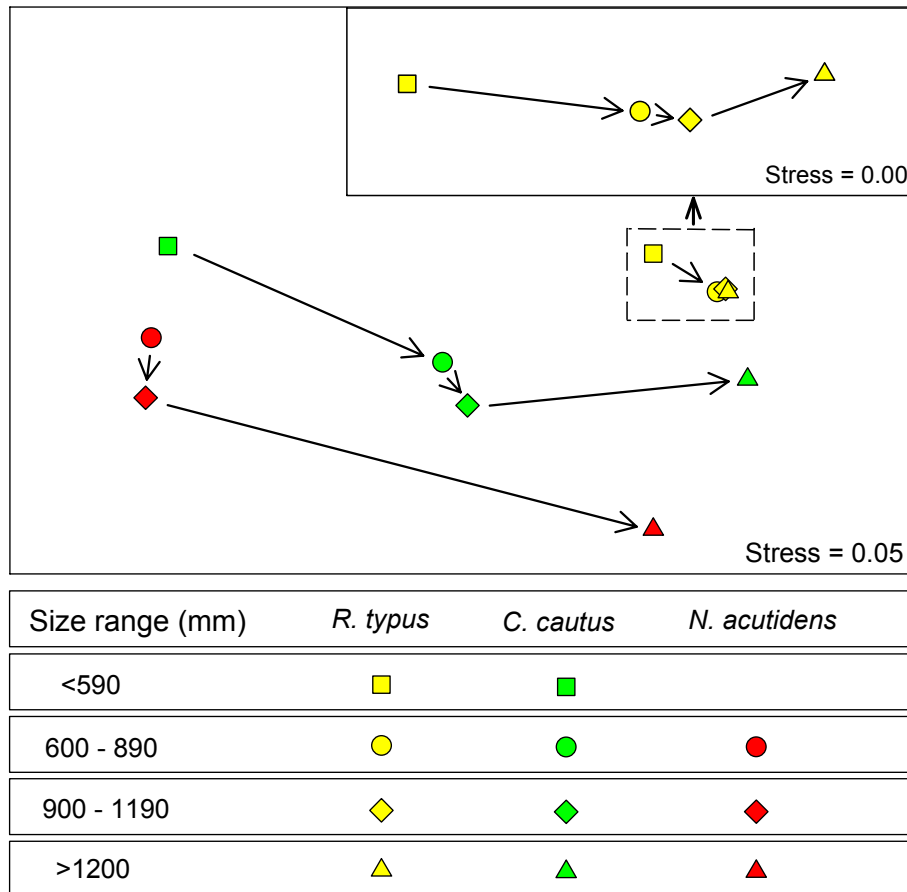


Figure 4.4 Non-metric multidimensional scaling ordination of the mean volumetric dietary data for the different length classes of *Rhinobatus typus*, *Carcharhinus cautus* and *Negaprion acutidens*. The points in the box represent those produced by ordination of the dietary data for *R. typus* on their own. Arrows are drawn between the points for the dietary samples for each successive length class.

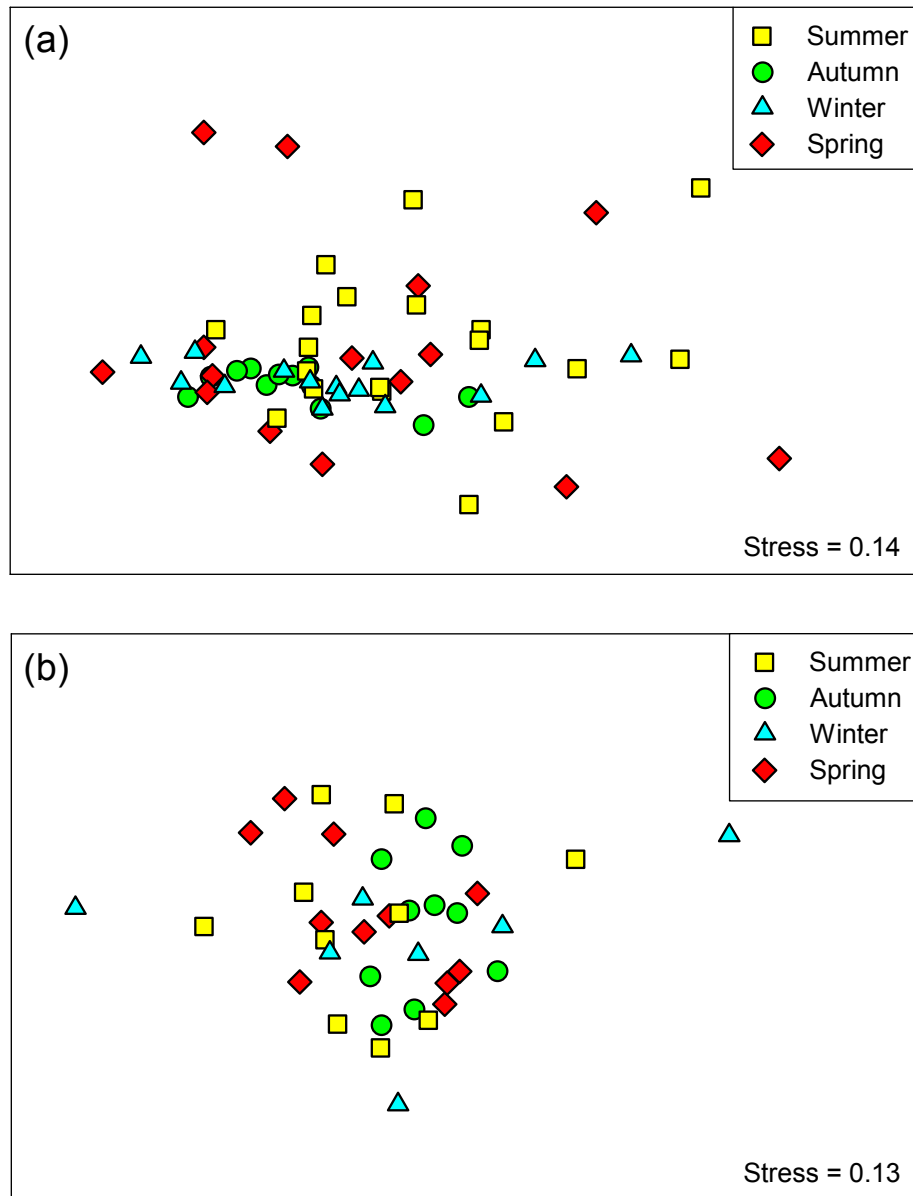


Figure 4.5 Non-metric multidimensional scaling ordination of the mean percentage volumetric dietary data for (a) *Rhinobatus typus* and (b) *Carcharhinus cautus* in each season, with each point (= dietary sample) representing meaned data for groups of five and three fish, respectively, that were randomly selected within each season.

respectively. ANOSIM showed that the dietary composition of *R. typus* differed significantly among seasons ($P < 0.05$; Global R statistic = 0.062). In the pairwise ANOSIM comparisons between seasons, the dietary composition of this ray in winter differed significantly from those in summer and spring ($P < 0.05$; R statistic = *ca* 0.105). SIMPER demonstrated that the dietary compositions of individuals in the former season were distinguished from those in the latter seasons by relatively greater abundances of portunids and penaeids.

Following ordination of the volumetric dietary data for *C. cautilus* in each season, the dietary samples for autumn tended to lie in the centre of the ordination plot, whereas those for each of the other seasons were distributed more widely throughout the plot (Fig. 4.5b). The samples for summer and winter were more widely distributed over the plot than those for spring and autumn, which is reflected in higher MVDISP values, *i.e.* 1.2 vs 0.85–0.88. Although a one-way ANOSIM indicated that there was a significant seasonal difference in the composition of the diets of *C. cautilus* ($P < 0.05$), the global R statistic was very low, *i.e.* 0.076, and none of the pairwise comparisons between the dietary compositions in the different seasons were significant ($P > 0.05$). Thus, as with *R. typus*, the R statistic values for pairwise comparisons are so low that the differences in dietary composition between seasons were very small.

4.4 Discussion

4.4.1 Partitioning of food resources amongst species

The results of this study demonstrate that the dietary compositions of the four most abundant species of elasmobranch in a subtropical embayment differed significantly from each other in all cases except for *Rhizoprionodon acutus* vs *Negaprion acutidens*. The

potential invertebrate and fish prey resources in Herald Bight are therefore, to a considerable extent, partitioned amongst these important predators. Thus, at a broad taxonomic level, the ray *Rhinobatus typus* fed almost exclusively on penaeid prawns and portunid crabs, whereas the three species of sharks ingested mainly teleosts.

The above dietary differences are consistent with the hypothesis that, due to morphological and behavioural differences, the prey ingested by the single species of ray, that was abundant in nearshore waters in Shark Bay, would differ markedly from that of the three species of shark that were likewise abundant in the same waters. Thus, the batoid *R. typus* has a relatively small mouth and lives on or just above the substrate surface, accounting for this species feeding almost exclusively on benthic invertebrates, *i.e.* juvenile prawns and crabs. Although another member of the same family, *Aptychotrema rostrata*, does consume a reasonable volume of teleosts in a large embayment located at a similar latitude on the east coast of Australia, crustaceans still constituted by far the most important component of its diet (Kyne & Bennett, 2002). Furthermore, since the feeding process of rhinobatids involves firstly immobilisation of their prey on the substrate surface, and then a repositioning of its body so that the mouth can be used to provide a suction and bite manipulation mechanism to ingest that prey (Wilga & Motta, 1998; Motta & Wilga, 2001), it is not suited to catching fast-moving prey, such as teleosts. In contrast, carcharhinids rely mainly on ram feeding, whereby fast swimming is used to attack and ingest their prey (Moss, 1972; Motta *et al.*, 1997; Motta & Wilga, 2001). This type of feeding, allied with the possession of large and powerful jaws with a large gape, explains why several more active teleost species made such a large collective contribution to the diets of *Carcharhinus cautus*, *R. acutus* and *N. acutidens* in the nearshore waters of Shark Bay. Although the first two species also ingest large volumes of teleosts and almost no penaeids in nearshore waters of the Gulf of Carpentaria in north-eastern Australia, *R. acutus* does

consume a substantial quantity of penaeids when it occupies the offshore waters of that gulf, where penaeids would presumably have been larger (Salini *et al.*, 1991).

Although each of the three species of shark consumed large volumes of teleosts in nearshore waters of Shark Bay, the contributions made by the various species of teleost to the diets of the three selachian species differed. Thus, platycephalids and terapontids were more important to the diets of *C. cautus* than to those of *R. acutus* and *N. acutidens*, whereas atherinids and clupeids made greater contributions to the diets of the latter two species. The diet of *C. cautus* was also distinguished from that of the other two shark species by the presence of reptiles, presumably sea snakes, which are abundant in Shark Bay, and, in comparison with that of *N. acutidens*, the absence of the ray *R. typus*. Although the dietary compositions of *R. acutus* and *N. acutidens* were not significantly different, it is noteworthy that, in Fig. 4.1, three of the five points for the dietary samples of *R. acutus* occupied the upper left quadrant of the ordination plot, where none of those of *N. acutidens* was located, and that three of the five samples of the latter species occupied the bottom third of the plot, where none of those of *R. acutus* was situated. Thus, although the dietary compositions of *R. acutus* and *N. acutidens* were not significantly different statistically, there was still evidence of some partitioning of prey amongst these two species.

Rhizoprionodon acutus differs from the other two species of shark, *C. cautus* and *N. acutidens*, in that it lives mainly over seagrass rather than over bare sand. It thus appears relevant that the centropomid *Psammoperca waigensis*, which is very abundant in seagrass but not over unvegetated substrate (Travers & Potter, 2002), was only ingested by *R. acutus*. Furthermore, the sparid *Rhabdosargus sarba*, which lives in unvegetated areas in Shark Bay (S.A. Hesp, in prep), was found in the stomach contents of *C. cautus* and

N. acutidens but not *R. acutus*. There are thus some indications of food partitioning among the three shark species that reflect differences in the habitats occupied by those species.

Although the major contribution made by teleosts to the diets of the three shark species in Herald Bight parallels the situation recorded for these species in the Gulf of Carpentaria (Salini *et al.*, 1991), the major families of teleosts that were ingested differed. For example, species of hemiramphids, mugilids and clupeids were the main teleosts consumed by the substantial numbers of *R. acutus* that had been caught in nearshore waters of the Gulf of Carpentaria (Salini *et al.*, 1991), whereas the first two of these families were not recorded in the diets of this species in Shark Bay. In contrast, the teleost component of the diets of *R. acutus* in Shark Bay was dominated by atherinids, clupeids, sillaginids and labrids, which are abundant in the nearshore waters of this embayment (Travers & Potter, 2002; M.B. Pember, unpublished data). The considerable diversity of teleosts ingested by *C. cautus*, *i.e.* 15 families, parallels the results of previous studies on the dietary compositions of carcharhinids in northern Australia (Lyle, 1987; Salini *et al.*, 1991; Stevens & McLoughlin, 1991; Simpfendorfer, 1998). The contribution made by cephalopods to the diets of *R. acutus*, *i.e.* 17.9%, is similar to that recorded for this species in northern Australia (Stevens & McLoughlin, 1991; Salini *et al.*, 1991). Although the dietary compositions of *R. typus* and *C. cautus* varied significantly among seasons, the analyses showed that these differences were very small. This lack of a conspicuous seasonal difference presumably reflects that the main prey of the four elasmobranch species remain at least moderately abundant throughout the year.

4.4.2 *Size-related changes in dietary compositions and dietary breadths*

The trends exhibited by the diets for the two species for which there were substantial data for each of the four size classes, *i.e.* *R. typus* and *C. cautus*, demonstrated that the dietary

composition of both of these species underwent size-related changes. Thus, the contribution made to the diet of *R. typus* by penaeid prawns declined progressively as this batoid increased in size, whereas that of portunid crabs, predominantly *Portunus pelagicus*, exhibited the opposite trend. This size-related shift in diet may reflect that *P. pelagicus* was, on average, slightly larger and has a harder exoskeleton than penaeids and would thus be more readily captured and ingested by the larger rays. The extreme domination of the diets of each length class of *R. typus* by just three species of crustacean accounts for the dietary breadth of each of these length classes being relatively low and less than the dietary breadths of each of the corresponding length classes of the three shark species. The smaller dietary breadth of the ray species is reflected in the fact that the points for the dietary samples on the ordination plot shown in Fig. 4.1 are far less widely dispersed than those for the three shark species. In the case of *C. cautus*, the size-related changes involved a progressive reduction in the contribution made to the diet by teleosts. Furthermore, the presence of a greater number of dietary categories in the two length classes that were well represented in samples, *i.e.* 600–890 and 900–1190 mm, is reflected in dietary breadths that are high and over twice those of the corresponding size classes of *R. typus*, which were each likewise represented by a large sample size. Ophidian reptiles, presumably sea snakes, were present in the diets of the largest length class of *C. cautus* in Shark Bay, paralleling the situation recorded for several shark species in northern Australia, *i.e.* *C. cautus*, *Carcharhinus melanopterus* and *Galeocerdo cuvier* (Lyle, 1987; Lyle & Timms, 1987; Simpfendorfer, 2001b).

Although *N. acutidens*, which was entirely represented by juveniles, fed mainly on teleosts, three of its largest individuals, with lengths 1390–1510 mm, also fed on the batoid *R. typus*, that is considerably larger than the teleosts, such as atherinids, which otherwise dominated the fish component of the diet of this shark species. Compagno (1984) also

records that *N. acutidens* feeds on dasyatids as well as teleosts. Although elasmobranchs were not recorded in the stomach contents of the *N. acutidens* examined by Salini *et al.* (1991) from the Gulf of Carpentaria, it appears highly relevant that the individuals examined by those workers were all less than 1260 mm in length. Elasmobranchs thus presumably tend only to become an important component of the diets of *N. acutidens* after that species has attained a certain size.

In summary, this study has demonstrated that the food resources in the nearshore waters of a large subtropical embayment are partitioned amongst the single species of ray and three species of shark that are abundant in those waters, which thereby reduces the potential for competition for those resources. The ray feeds almost exclusively on penaeid and portunid crustaceans and thus, in this respect, differs markedly from the three shark species which all consume large volumes of teleosts, with the precise species varying amongst those selachians. Since the diets of each species undergo size-related changes, the food resources are spread within as well as amongst the four species of elasmobranch.

CHAPTER 5

Size and age compositions and reproductive biology of the nervous shark

***Carcharhinus cautus* in a large subtropical embayment, including an**

analysis of growth during pre- and postnatal life

5.1 Introduction

Although *Carcharhinus* is a speciose and widely-distributed genus, there have been few studies of the age compositions and growth of its various species. However, the ages of individuals of *Carcharhinus tilstoni* and *C. sorrah* in northern Australian waters have been determined and the resultant length-at-age data used to construct von Bertalanffy growth curves (Davenport & Stevens, 1988). Although the ages at length zero of these species, *i.e.* t_0 , were less than zero in the von Bertalanffy growth equations, as would be expected when the age at parturition was set as age 0, they were still, in most cases, appreciably greater than the duration of embryonic life. This implies that the rate of growth in the period prior to birth, when a considerable amount of growth occurs, was more rapid than would be accommodated by the von Bertalanffy growth equation.

Recent studies have demonstrated that the mean size (disc width) at parturition of individuals of another group of elasmobranchs, namely the myliobatiforms *Urolophus lobatus*, *Trygonopectera personata* and *T. mucosa*, represented between 33 and 52% of their asymptotic disc widths (White *et al.*, 2001, 2002). Thus, in the case of the two *Trygonopectera* species, it was decided to ascertain whether it was possible to use a single smooth curve to describe the pattern of growth of the females and males of these species throughout the whole of their prenatal and postnatal life. Although the von Bertalanffy growth curve fitted most of the latter data well, it passed below the points for the lengths at age of the very largest females. This slight deficiency was overcome by using the Schnute growth curve (Schnute, 1981) that incorporates four parameters rather than the three that are present in the von Bertalanffy growth equation.

The first aim of this study was to determine the age compositions of the females and males of the nervous shark *Carcharhinus caudatus*, and to use the resultant length-at-age data to construct growth curves for both sexes of this species. Since this species gives birth at a

relatively large size (Lyle, 1987), the pattern of growth throughout the whole of life from conception, as well as throughout just postnatal life, has been determined. Growth was initially analysed using the von Bertalanffy growth equation, as is typically employed for describing growth in elasmobranchs (*e.g.* Branstetter, 1987a, Simpfendorfer, 1993, Lessa *et al.*, 1999). Although the resultant growth curves for females fitted well most of the lengths at age of individuals, they passed below the points for the larger fish, as was also the case with the two *Trygonoptera* species (White *et al.*, 2002). The Schnute growth equation has thus likewise been used to ascertain whether it provided a significantly better fit to the lengths-at-age data for this species. However, since the likelihood ratio test, that is used to compare growth curves, is very sensitive when, as in the current study, the number of points for the lengths at age are large, the question of whether it is desirable to shift to a more complex and far less widely-used equation has been explored.

Emphasis was placed initially on elucidating the timing of reproductive events and the sizes attained by embryos at regular intervals to determine accurately the pattern of growth of female and male *C. cautus* throughout the whole of life after conception. Since the timing of reproductive events is likely to be influenced by water temperature, the data on the reproductive biology have been compared with those of Lyle (1987), who studied *C. cautus* in a far more northern and thus warmer part of Australia.

5.2 Materials and Methods

5.2.1 Sampling regime

Details of the sampling regime and gear utilised to catch individuals of *Carcharhinus cautus* in Shark Bay are given in Chapter 2. The entire reproductive tract of each mature female was removed and frozen for subsequent examination in the laboratory. In the case of males, a note was kept on whether their claspers were calcified and, if so, to what extent.

The lengths of claspers, measured from posterior end of cloaca to the tip, were recorded to the nearest 1 mm. A section of six vertebrae was removed from that part of the vertebral column that was located in the region of the first dorsal fin and then frozen.

5.2.2 *Reproductive biology*

The maturity stage of each individual shark collected from Shark Bay was recorded. Females that contained large, yolked oocytes in their right ovary and possessed well-developed uteri, but which were not pregnant, were recorded as mature non-pregnant, whereas those with either intrauterine eggs or embryos were recorded as mature pregnant. Females possessing enlarged but flaccid and empty uteri were termed post-partum. All other females, including those containing ovarian follicles undergoing vitellogenesis and uteri that were not yet fully developed, and which were thus not yet capable of reproduction, were recorded as immature. Males were considered mature when their claspers were enlarged and fully calcified. Recently-born sharks could be distinguished by the presence of an umbilical scar on their ventral body surface in the region between the pectoral fins.

The presence of any bruised claspers on males and fresh bite marks on the sides of females was taken as indicating that mating had recently occurred. Males were recorded as spent when their testes were enlarged but flaccid and their seminal vesicles were enlarged but empty. Data for the above variables were used to determine the approximate time of copulation.

The diameter of the single largest oocyte in the right ovary of each mature female, *i.e.* the maximum oocyte diameter (MOD), was measured to the nearest 0.1 mm, whereas the length of all intrauterine embryos were measured to the nearest 1 mm. An example of a mature, pregnant reproductive tract is shown in Plate 5.1 and of the umbilical scar on the

ventral body surface of a recently-born shark is shown in Plate 5.2. The intrauterine embryos of *C. cautus* could generally be sexed once they were 1–2 months old and *ca* 100 mm in length.

The lengths at which 50% of both females and males of each species attain maturity (*i.e.* the L_{50} at first maturity) were derived by fitting the logistic function,

$$p_L = \frac{1}{1 + \exp\left[-\ln(19)\frac{(L - L_{50})}{(L_{95} - L_{50})}\right]},$$

to the proportion, p_L , of those sharks that were mature at length L , where L_{50} and L_{95} are constants and \ln is the natural logarithm. Maximum likelihood estimates of the parameters were obtained using the routine SOLVER in Microsoft™ Excel and calculating the likelihood of immature and mature individuals as $1 - p_L$ and p_L , respectively. The reported estimates of the parameters were determined as the median values derived from 200 sets of the randomly resampled data, with the same sample size, drawn from the data on observed maturity status at length for female and male sharks, respectively. The approximate 95% confidence intervals were estimated as the 2.5 and 97.5 percentiles of the 200 estimates resulting from the resampled data.

5.2.3 Age and growth

Two adjacent vertebral centra were separated from the extracted part of the vertebral column of each *C. cautus* examined and their cartilaginous processes and surrounding connective tissue removed. They were then soaked in 5% sodium hypochlorite for 5 to 20 min, depending on their size (Simpfendorfer, 1993; White *et al.*, 2001), washed and allowed to dry. Each centrum was mounted in clear epoxy resin and cut into 0.3–0.4 mm sections using a low-speed Isomet diamond saw. The sections were moistened with distilled

water to enhance the definition of the opaque zones and then, using a dissecting microscope, examined against a black background under reflected light. The opaque zones in the two adjacent centra selected from each vertebral column were counted to confirm that the number of opaque zones visible in each centrum was the same, after which one of these centra was selected for future use. The sections were stored by mounting on glass slides using DePX mounting medium.

The distance between the outer edge of the outermost opaque zone and the periphery of each centrum, *i.e.* the marginal increment, was measured. When only one opaque zone was present, the distance between the nucleus and the outer edge of that zone was measured. In contrast, when more than one opaque zone was present, the distance between the outer edges of the two outermost zones was measured. All measurements were made to the nearest 0.05 mm along the vertical axis of the centrum and thus perpendicular to the opaque zone(s). The marginal increment on each centrum was then expressed as a proportion of the distance between the nucleus of the centrum and the outer edge of the opaque zone, when only one such zone was present, or as a proportion of the distance between the outer edges of the two outermost opaque zones, when two or more such zones were present.

von Bertalanffy growth curves were fitted to the individual lengths of each female and male at their estimated age at capture, firstly by including only the lengths of postnatal individuals and employing the date of parturition as age 0, and then by including those of both embryos and postnatal individuals and using the conception date as age 0 and thus encompassing growth during both prenatal and postnatal life. The data were fitted by minimizing the sum of squared deviations between observed and predicted lengths using a nonlinear regression in SPSS (SPSS Inc., 1999) and the routine SOLVER in Microsoft™ Excel. The von Bertalanffy growth equation is

$$L_t = L_\infty \left(1 - e^{-k(t-t_0)}\right),$$

where L_t is the length at age t , L_∞ is the mean asymptotic length, k is the growth coefficient and t_0 is the age at which the estimated length is zero.

The Schnute growth equation (see below) was fitted to the same length-at-age data as the von Bertalanffy growth equation.

$$L_t = \left[L_1^b + (L_2^b - L_1^b) \frac{1 - e^{-a(t-\tau_1)}}{1 - e^{-a(\tau_2-\tau_1)}} \right]^{1/b} \quad (\text{Schnute, 1981, Equation 15}),$$

where L_1 and L_2 are the estimated lengths at selected reference ages τ_1 and τ_2 years and a and b are constants (both $\neq 0$). From this equation, the asymptotic length can be calculated using the equation

$$L_\infty = \left[\frac{e^{a\tau_2} L_2^b - e^{a\tau_1} L_1^b}{e^{a\tau_2} - e^{a\tau_1}} \right]^{1/b} \quad (\text{Schnute, 1981}).$$

The theoretical age at which the estimated length is zero, *i.e.* t_0 , was determined from

$$t_0 = \tau_1 - \frac{1}{a} \ln \left\{ 1 + \frac{L_1^b (1 - e^{-a(\tau_2-\tau_1)})}{L_2^b - L_1^b} \right\}$$

It was assumed that, when fitting all growth curves, $L_t = 0$ if the age of an individual lay below t_0 .

A runs test was applied using SPSS to the residuals from each of the analyses to determine whether the growth curves deviated systematically from the observed data. Before applying this test, the lengths-at-age were sorted by age in years and then randomly within age.

The von Bertalanffy and Schnute growth curves derived for female and male *Carcharhinus caudatus*, using firstly the lengths-at-age for postnatal fish and then the combined lengths-at-age for embryos and postnatal fish, were compared using a likelihood

ratio test to determine whether there were significant differences between the curves derived for each sex using the different growth equations and between the curves derived for both sexes using the same growth equations (Kimura, 1980). The null hypothesis, ω , that the growth curves could be described by equations with q linear constraints on the parameters was compared with the alternative hypothesis, Ω , that the parameters for the two curves were distinct. The log-likelihood was determined for the null hypothesis and for the alternative hypothesis as λ_{ω} and λ_{Ω} , respectively, where each was calculated, ignoring constant terms, from the associated sum of squared deviations SS over the n observations, as

$$\lambda = -\frac{n}{2} \ln\left(\frac{SS}{n}\right).$$

Next, the test statistic for the likelihood ratio test was calculated as $2(\lambda_{\Omega} - \lambda_{\omega})$. The null hypothesis was rejected at the $\alpha = 0.05$ level of significance when the test statistic exceeded $\chi^2_{\alpha}(q)$ (e.g. Cerrato, 1990).

The absolute differences between the lengths at age, estimated from the von Bertalanffy and Schnute growth curves for the fish throughout all ages from t_0 , were determined and expressed as a percentage of the length calculated for each age using the von Bertalanffy equation. The curves were considered sufficiently different to warrant considering adopting the Schnute curve, rather than the von Bertalanffy curve, if the maximum percentage for this measure at any point exceeded 5%. Fish less than age 1 were excluded from this analysis as this differential measure is very sensitive to small differences between the lengths estimated for the smallest fish from the growth curves. Considerations of the potential value of using the Schnute curve also took into account other comparisons between the curves, such as the values for the coefficient of

determination, t_0 and L_∞ , and whether the runs test revealed any structural problems with the growth curve.

5.3 Results

5.3.1 *Environmental data*

Mean monthly temperatures at the three gillnet sampling sites (NV, SM and DM) close to shore at Herald Bight increased from 29.4°C in January to a maximum of 33.5°C in March, and then declined to a minimum of 17.2°C in June (see Fig. 3.1 in Chapter 3). Although the water temperatures in the shallow seagrass sampling site (SG) further offshore at Herald Bight followed similar trends to the sites close to shore, they did not vary to the same extent, *i.e.* ranged by only 8.0°C, compared with 16.3°C along the shoreline.

5.3.2 *Reproductive biology*

Although only a small number of mature, non-pregnant females were caught, the mean monthly MODs in the right ovary of such females still showed a clear trend throughout the year, with values declining from 10–11 mm in December and January to *ca* 5 mm in March, before rising to >20.5 mm in September, October and November (Fig. 5.1).

Although the majority of large yolked oocytes had already been ovulated by December, one or two residual large ova, with diameters ≥ 20.0 mm, were retained, both in that month and also January, by those females that had recently become pregnant (Fig. 5.1). Since large oocytes were not present in pregnant females in subsequent months, the few large oocytes found in pregnant females in mid- to late summer would presumably have been either ovulated or resorbed in the subsequent months. The mean monthly MODs of the second and quite distinct cohort of small oocytes present in the right ovary of females in December

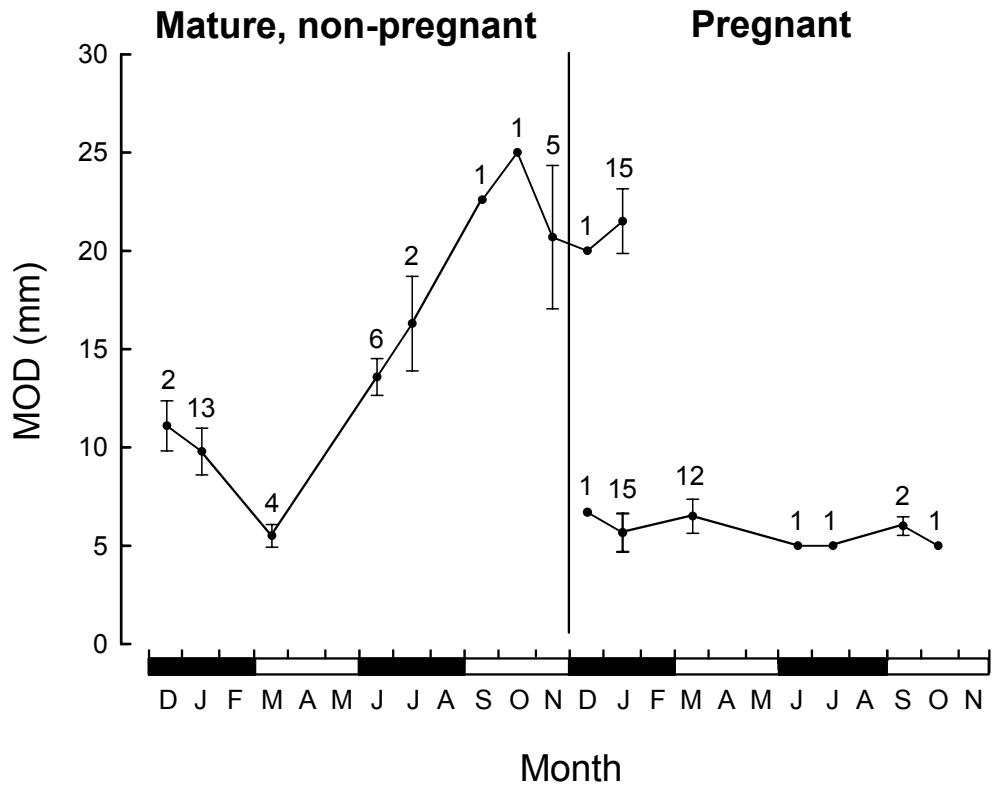


Figure 5.1 Mean monthly maximum oocyte diameters (MOD) \pm 1 SE in the ovary of mature, non-pregnant females of *Carcharhinus cautus*.

and January were much lower, *i.e.* 6.7 and 5.7 mm, respectively. The MODs of pregnant females were 6.5 mm in March and remained low in all subsequent months. Thus, since the majority of oocytes in mature, non-pregnant females had been ovulated by late November and recently-pregnant females with very small embryos were first caught in December (Fig. 5.2), 1 December was assigned as the date of both ovulation and conception. This date was used as age 0 for calculating the lengths-at-age of female and male fish for constructing the growth curves that encompassed the whole of pre- and postnatal life in both sexes.

During November and early December, some of the mature females bore fresh bite marks on their sides and the majority of the mature males were spent and had bruised claspers. This provides strong circumstantial evidence that this species copulates mainly in late October–early November and thus just prior to ovulation.

The mean lengths of embryos increased from 15 mm in December, when embryos were first found, to 228 mm in April and then to a maximum of 333 mm in October (Plates 5.3, 5.4, Fig. 5.2). The attainment by embryos of their maximum size in October and the absence of embryos *in utero* in November, strongly indicates that parturition typically occurs in late October and early November. Therefore, 1 November was assigned as the date of parturition (age 0) for calculating von Bertalanffy growth curves during postnatal growth. This estimate of the time of parturition is consistent with the presence of large numbers of small juvenile *C. cautus* in the shallow waters of Herald Bight in November and December and that the lengths of these in a subsample from the latter month, *i.e.* 420 to 450 mm, were only about 100 mm greater than the maximum mean monthly length of the embryos.

The mean litter size of *Carcharhinus cautus* is 4.2, *i.e.* 2.1 per uterus, with the number of young in females ranging from 2 to 6. There was no obvious relationship between the number of embryos and the total body length of *C. cautus* ($R^2 = 0.006$).

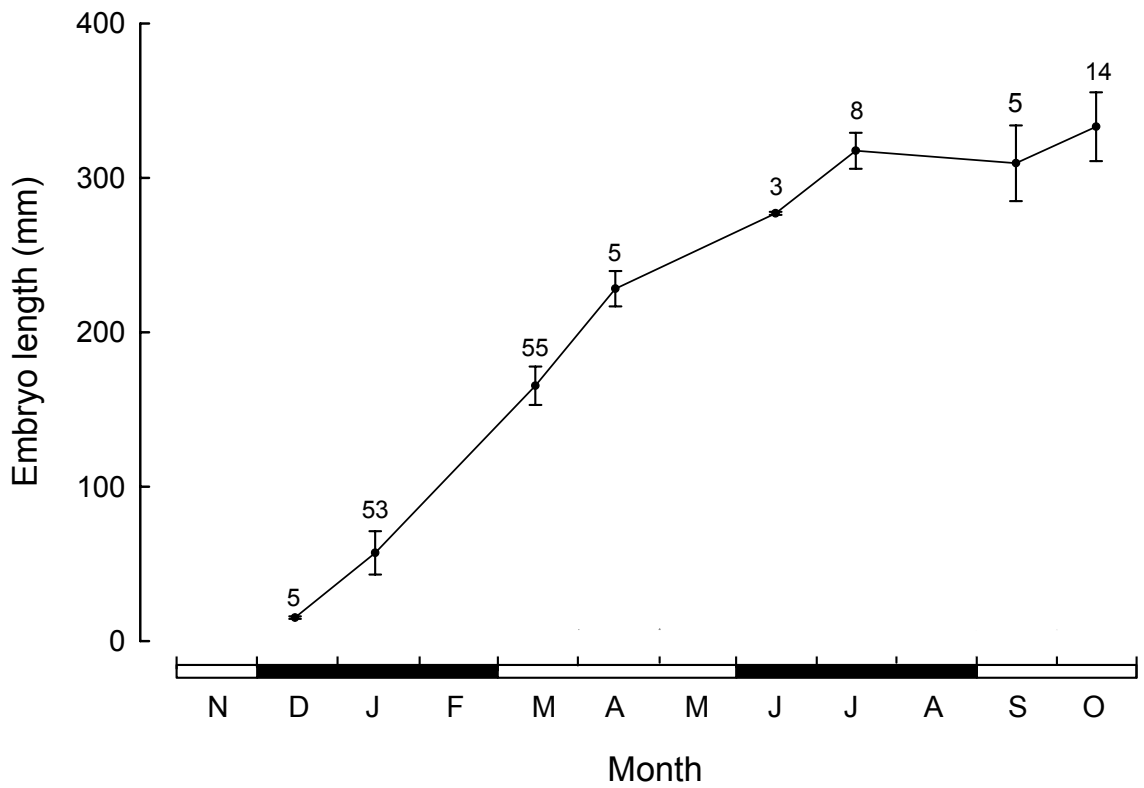


Figure 5.2 Mean monthly total lengths \pm 1 SE of *in utero* embryos of *Carcharhinus cautus*. Number of embryos measured in each month is given above each mean.

Although the percentage of females amongst mature individuals was much greater than that of males in most months of the year, this percentage was close to parity in spring when this species copulates. This indicates that, when copulation is not occurring, the mature males move to different areas than mature females, in which context it appears relevant that only mature males were caught in seagrass on the four occasions that this habitat type was sampled.

5.3.3 *Validation of the ageing procedure*

The mean monthly marginal increments on vertebral centra of *Carcharhinus cautus* with either 2 or 3 opaque zones increased from *ca* 0.45 in January to their maxima of 0.55 to 0.75 in July to September and then fell to their minima of *ca* 0.3 in October (Fig. 5.3). The mean monthly marginal increments on centra with 4 or more opaque zones followed the same trend, increasing from *ca* 0.5 in January to reach a peak of *ca* 0.9 in September, before declining precipitously to *ca* 0.1 in October and then increasing to *ca* 0.5 in December (Fig. 5.3). Although individuals with vertebral centra possessing only 1 opaque zone were not found in some months and were in low numbers in some other months, the mean monthly marginal increments of such centra were still clearly greatest in winter and least in mid-spring and thus apparently followed the same trends as those on centra in which there were two or more opaque zones. Since the marginal increments on vertebral centra with two or more opaque zones, and probably also on those with a single opaque zone, declined precipitously only once during the year and then rose progressively to reach a peak in winter, only one opaque zone becomes delineated annually on the centra of *C. cautus*. Thus, the number of such opaque zones on these centra can be used to help determine the age of this species.

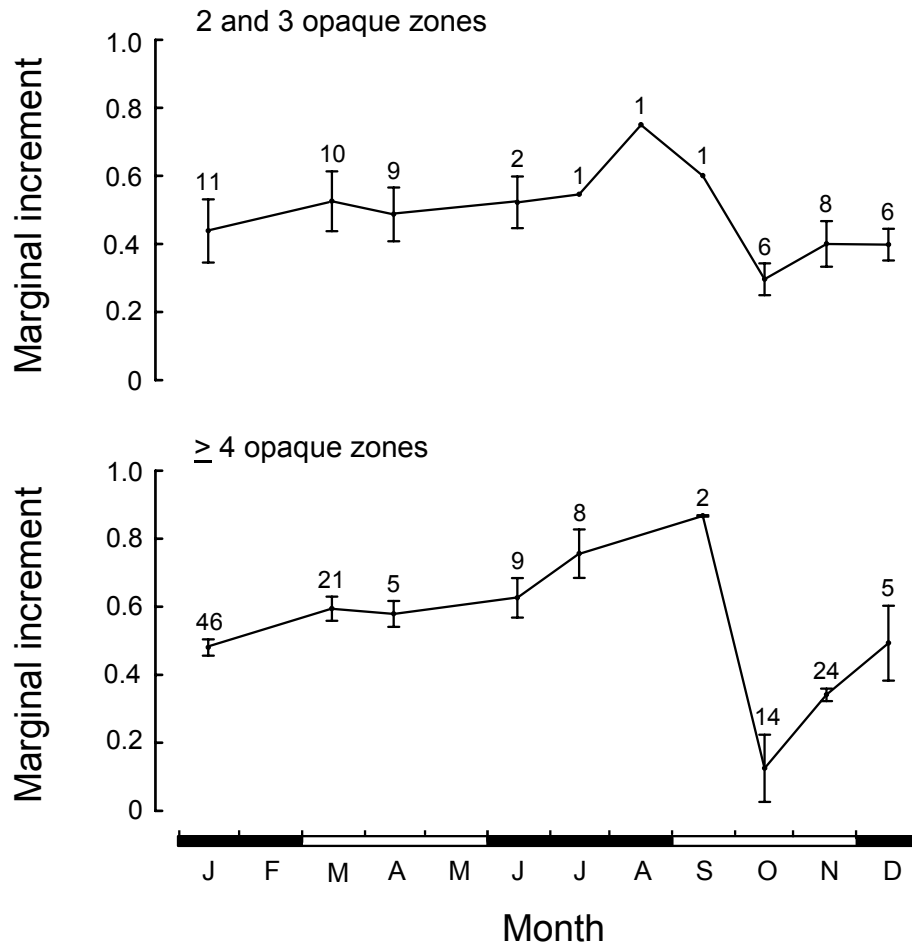


Figure 5.3 Mean monthly marginal increments ± 1 SE for vertebral centra of *Carcharhinus cautus* with either 2 or 3 or ≥ 4 opaque zones. Sample size for each month is given above each mean. Note that marginal increments are recorded as a proportional value (see Materials and Methods).

5.3.4 *Size and age compositions*

Since *Carcharhinus cautus* undergoes such a relatively large amount of growth in the 11 months between conception and parturition, it was decided, in the following account of the length distributions of the different age classes of this species, to regard the 0+ age class as commencing at conception. Thus, since gestation lasts for 11 months, the 0+ age class corresponds to *in utero* individuals in all but the last month of the first year of life.

The 0+ age class of *C. cautus* was first found in summer, when its modal length class was only 100–149 mm (Fig. 5.4). The modal length of the females and males of this cohort increased to 200–249 mm in autumn and to 300–349 and 350–399 mm, respectively, in spring. In summer, the early 1+ females and males of *C. cautus*, *i.e.* the recently-born juveniles, were represented by a modal length class of 450–499 mm and their length distributions were discrete from those of subsequent age classes (Fig. 5.4). The absence of an opaque zone in the vertebral centra of these fish shows that no opaque zone was laid down during the preceding winter when this species was still an embryo. However, a single opaque zone was clearly present in those fish that, in summer, were slightly larger than the 1+ age class. Thus, the first zone is laid down in the first winter after parturition.

The distribution of the lengths of age classes 2 and above overlapped (Fig. 5.4). The length-frequency distributions demonstrated that, amongst the older fish, *i.e.* ≥ 6 years, the females were both more abundant and attained larger sizes. The maximum observed lengths were 1330 mm for a female of 16.4 years and 1110 mm for a male of 9.0 years.

5.3.5 *Growth curves*

The runs test failed to detect a structural deficiency in the von Bertalanffy growth curve fitted to the lengths-at-age of postnatal females of *C. cautus* ($P < 0.05$), which is consistent with the visual observation that this curve provided a good fit to the lengths-at-age

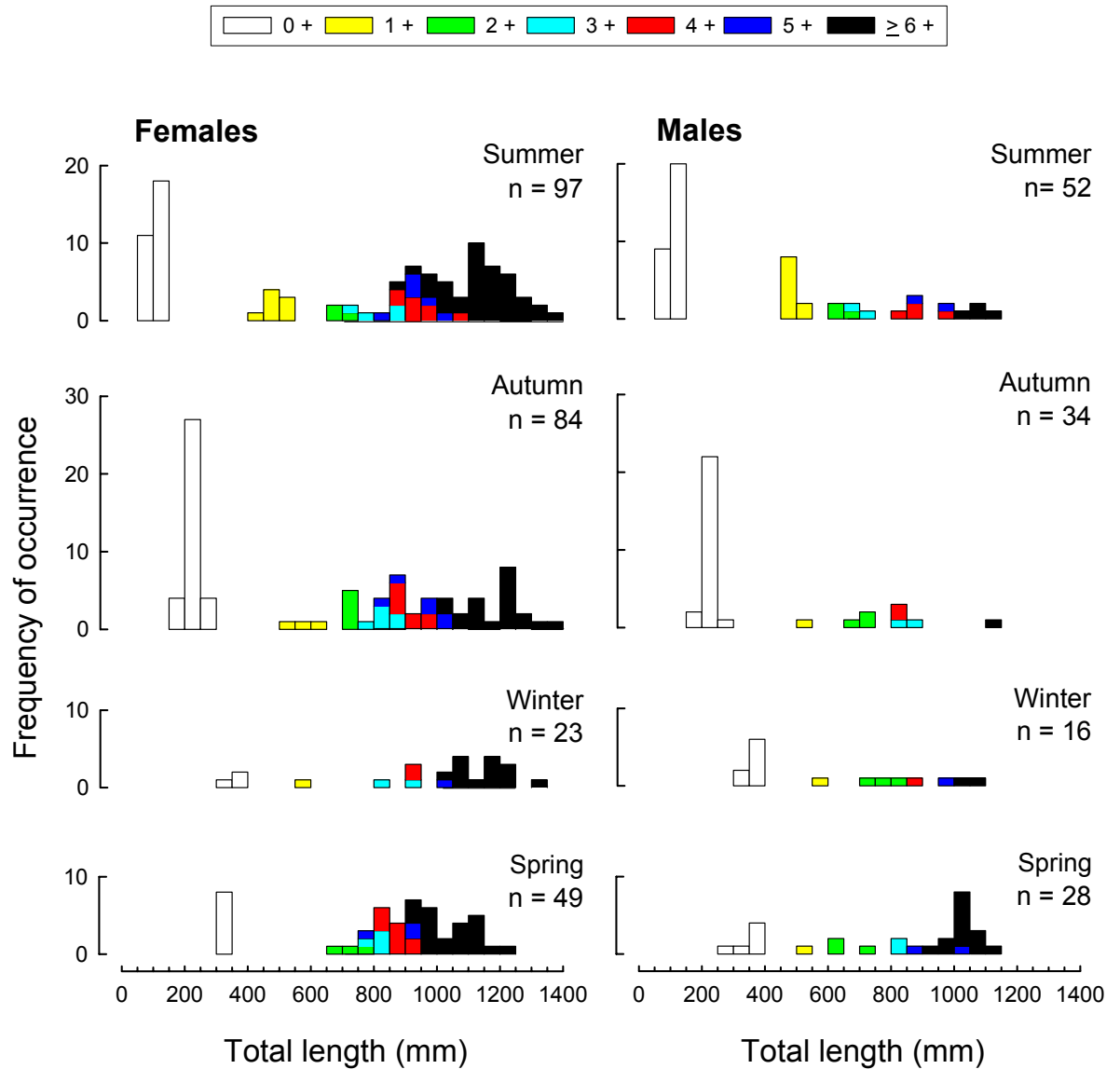


Figure 5.4 Length-frequency histograms for different age classes of females and males of *Carcharhinus cautus* in the four seasons using data for the whole sampling period. n = number of fish caught. Ages are recorded from conception.

throughout most of the age range of these fish (Fig. 5.5a). However, the curve did tend to pass above the lengths-at-age of recently-born fish and below the lengths-at-age of the very oldest fish (Fig. 5.5a), which would help account for the coefficient of determination (R^2) being slightly less than 0.900. The poor fit at the extreme lower end of the age range, and the fact that the lengths of prenatal individuals were not included, also accounts for the age at length zero (t_0) being -32.5 months rather than -11 months, the value that would be expected on the basis of the duration of the gestation period. The likelihood ratio test demonstrated that the Schnute growth curve significantly improved ($P < 0.001$) the fit to the length-at-age data for postnatal females from that obtained using the von Bertalanffy equation (*cf* Figs 5.5a, c). Furthermore, the runs test failed to detect any major structural problems with the Schnute growth curve for these data ($P > 0.05$). The Schnute growth curve overcame the deficiencies at the very upper and very lower ends of the age range (*cf* Figs 5.5a, c). The improvement in the fit by using the Schnute growth curve is emphasised by the coefficient of determination increasing from 0.892 to 0.919 (Table 5.1, 5.2). It also resulted in a very marked increase in the L_∞ from 1242 to 2238 mm (*cf* Tables 5.1, 5.2). The Schnute growth curve passed upwards and over the von Bertalanffy growth curve to produce a maximum difference of 5.0% at 1.3 years, before passing back below that curve to produce a maximum difference of only 1.9% at 7.3 years and then rising again above that curve to produce a maximum difference of 4.5% at 16.4 years.

In contrast to the situation for females, the fits to the lengths-at-age of postnatal males by the von Bertalanffy and Schnute growth curves were visually almost indistinguishable and had the same coefficients of determination and very similar L_∞ s (Table 5.1, 5.2). This point is emphasised by the maximum difference between

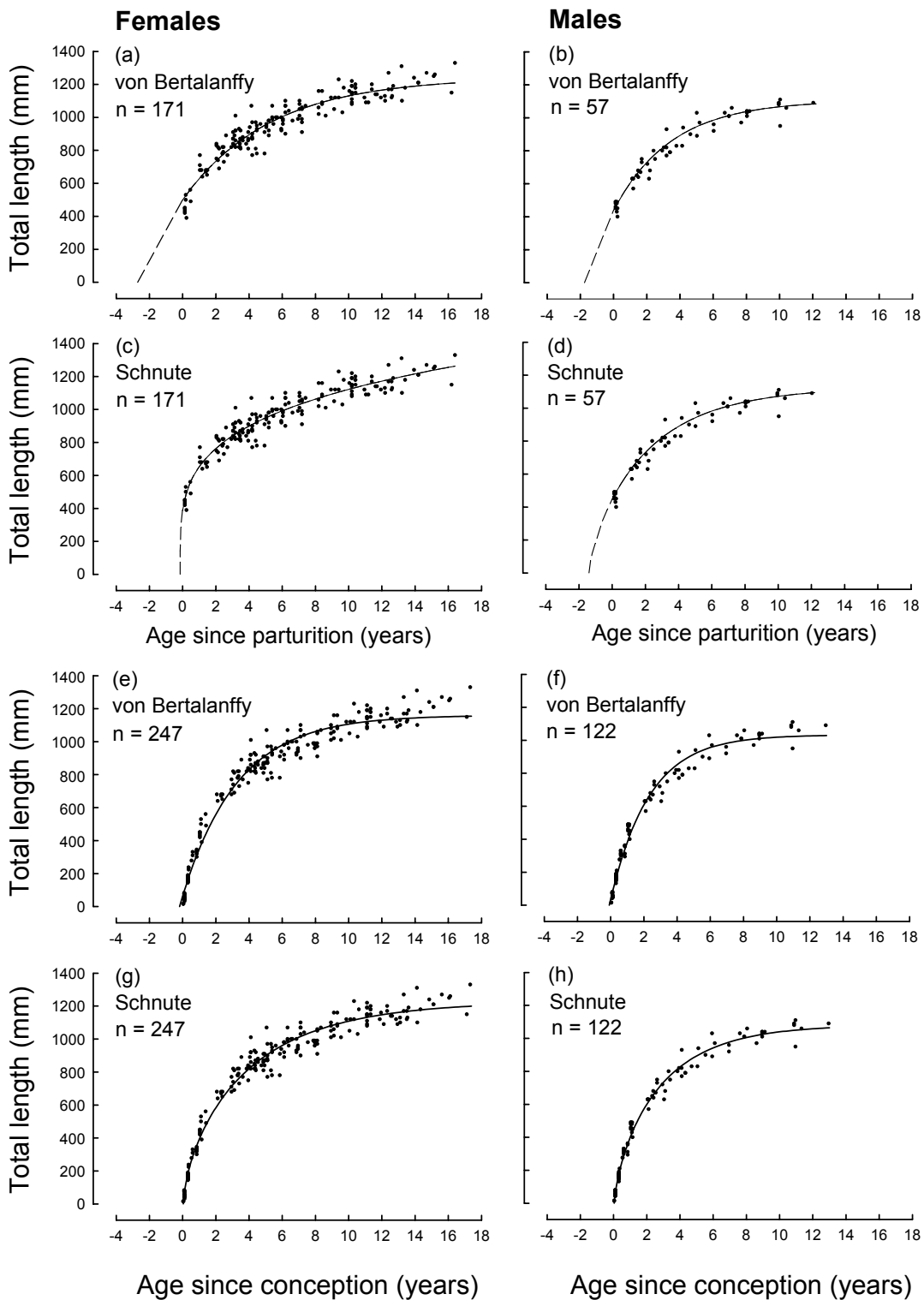


Figure 5.5 von Bertalanffy and Schnute growth curves fitted to lengths-at-age of female and male *Carcharhinus cautus*, using in (a) to (d) data solely from the time of parturition, *i.e.* during just postnatal life, and in (e) to (h) data from the time of conception, *i.e.* throughout both prenatal and postnatal life. The parameters for the von Bertalanffy and Schnute growth equations for females and males are provided in Tables 5.1 and 5.2, respectively. NB. Age 0 corresponds to the date of parturition in (a) to (d) and to the date of conception in (e) to (h).

the lengths at any age estimated from the two growth equations never exceeding 0.83%. Furthermore, the runs test demonstrated that the structure of the von Bertalanffy growth curve was appropriate ($P>0.05$). Thus, as would be expected, the curves were not significantly different ($P>0.05$) (Figs 5.5b, d) and there was no advantage in using the Schnute growth curve rather than the von Bertalanffy growth curve.

Table 5.1 von Bertalanffy growth parameters for females and males of *Carcharhinus cautus*, including upper and lower 95% confidence limits, derived from lengths-at-age of individuals during just postnatal life and using the parturition date as age 0, and for those throughout pre- and postnatal life and employing the conception date as age 0. L_{∞} , asymptotic length; k , growth coefficient; t_0 , hypothetical age at length zero; R^2 , coefficient of determination; n , sample size.

		von Bertalanffy parameters				
		k (year ⁻¹)	L_{∞} (mm)	t_0 (years)	R^2	N
Postnatal life						
	Estimate	0.190	1242	-2.71	0.892	171
Females	Upper	0.220	1285	-2.15		
	Lower	0.160	1199	-3.26		
	Estimate	0.287	1105	-1.75	0.953	57
Males	Upper	0.345	1155	-1.36		
	Lower	0.229	1055	-2.15		
Pre- and postnatal life						
	Estimate	0.300	1161	-0.183	0.976	247
Females	Upper	0.320	1182	-0.127		
	Lower	0.281	1140	-0.241		
	Estimate	0.427	1033	-0.081	0.986	122
Males	Upper	0.459	1056	-0.043		
	Lower	0.395	1010	-0.118		

The von Bertalanffy growth curve provided a good fit to the lengths-at-age for females throughout the majority of their pre- and postnatal life, *i.e.* from conception (Fig. 5.5e), which is consistent with the relatively high R^2 of 0.976 (Table 5.1). However, the runs test showed that this curve had some structural deficiencies ($P<0.001$), which would

be explained, at least partly, by the fact that this curve passed below most of the lengths of the very oldest fish. The use of the Schnute rather than the von Bertalanffy growth equation significantly improved ($P < 0.001$) the description of the growth of females during the whole of their pre- and postnatal life, $R^2 = 0.983$ (Fig. 5.5g), and the runs test suggested that this curve was appropriate for these fish ($P > 0.05$). The changes brought about by the use of a Schnute rather than a von Bertalanffy growth equation were reflected in an increase in the L_∞ from 1161 to 1308 mm (Tables 5.1, 5.2). The Schnute growth curve passed upwards and over the von Bertalanffy growth curve, before passing back below that curve to produce a maximum difference of only 3.1% at 6.1 years and then rising again above that curve to produce a maximum difference of 6.0% at 17.3 years.

Although the runs test suggested that there were structural deficiencies in both the von Bertalanffy and Schnute growth curves fitted to the lengths-at-ages of individual male fish throughout life (both $P < 0.01$), the R^2 for both of these two growth curves were high, *i.e.* 0.986 and 0.991, respectively (Tables 5.1, 5.2). The Schnute growth curve provided a slightly better fit than the von Bertalanffy growth curve ($P < 0.001$), by bringing about, in particular, a slight reduction in the location of the curve for the middle part of the age range and an elevation in its position for the very oldest fish (*cf* Figs 5.5f, h). The Schnute growth curve passed upwards and over the von Bertalanffy growth curve, before passing back below that curve to produce a maximum difference of only 3.6% at 3.6 years and then rising again above that curve to produce a maximum difference of 4.3% at 13 years.

Irrespective of whether the von Bertalanffy or Schnute growth equations were used, the four corresponding growth curves for females and males shown in Fig. 5.5 were always significantly different ($P < 0.001$).

Table 5.2 Schnute growth parameters for females and males of *Carcharhinus cautus*, including upper and lower 95% confidence limits, derived from lengths-at-age of individuals during just postnatal life, and using the parturition date as age 0 and for those throughout pre- and postnatal life and employing the conception date as age 0. L_1 and L_2 are lengths at selected reference ages τ_1 (3) and τ_2 (12) years; a and b are constants (both $\neq 0$); L_∞ , asymptotic length; R^2 , coefficient of determination; n , sample size.

		Schnute parameters						
		L_1 (mm)	L_2 (mm)	a	b	L_∞ (mm)	R^2	N
Postnatal fish								
	Estimate	839	1172	0.007	3.99	2238	0.919	171
Females	Upper	852	1188	0.079	5.12			
	Lower	827	1157	-0.067	2.85			
	Estimate	822	1093	0.229	1.57	1129	0.953	57
Males	Upper	842	1145	0.436	3.53			
	Lower	802	1041	0.023	-0.40			
Pre- and postnatal fish								
	Estimate	731	1151	0.121	2.16	1308	0.983	247
Females	Upper	743	1164	0.156	2.44			
	Lower	719	1138	0.085	1.88			
	Estimate	730	1066	0.261	1.53	1098	0.991	122
Males	Upper	743	1089	0.304	1.66			
	Lower	717	1044	0.218	1.40			

5.3.6 Size and age at maturity

The smallest mature female and male of *C. cautus* were 910 and 890 mm length, respectively. Maturity was attained by almost all females by the time they had reached a length of 1050 mm and by all males by the time they had reached a length of 950 mm. The L_{50s} (95% confidence intervals) for first maturity of females and males were 1007 (982–1025) mm and 913 (873–939) mm, respectively (Fig. 5.6).

Females and males first reached maturity at age five and four, respectively (Fig. 5.6). Although a few females did not attain maturity until they were nine years old, all of the males had become mature by the time they were five years old.

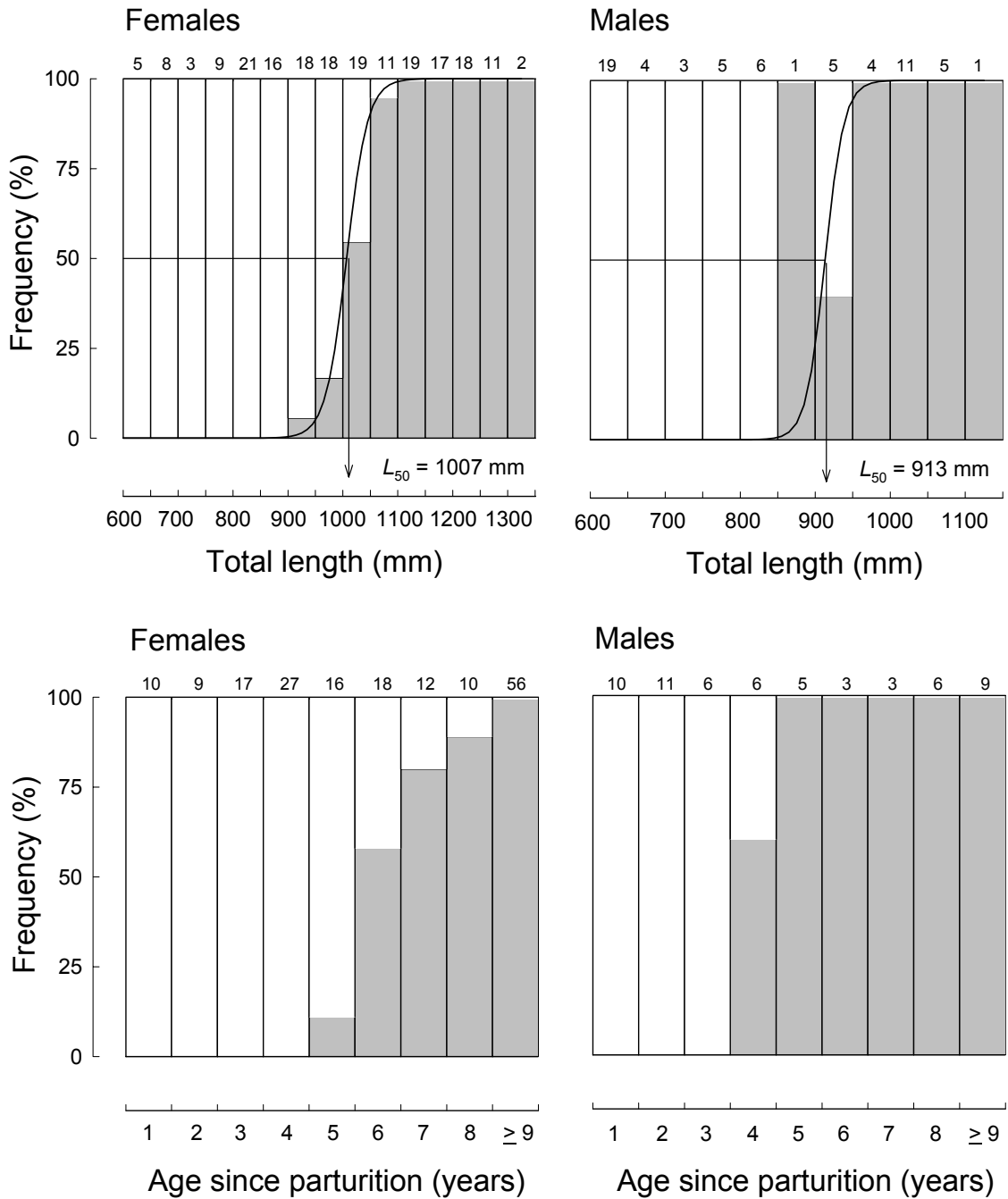


Figure 5.6 Percentage frequency of occurrence of immature and mature sharks in each sequential 50 mm length class and each sequential age class of female and male *Carcharhinus cautus*. The logistic curves for the length data were derived from the percentage contributions of mature sharks in sequential size classes. Arrows indicate position of the L_{50} . Samples sizes are given above each bar.

5.3.7 Length–mass relationships

The equations relating total length (L) and mass (M) of female and male *C. cautus* from Shark Bay are presented below, thus enabling approximate masses of sharks to be estimated from a given total length.

Females: $\text{Log}_{10} M = -4.47 + 2.85 \text{Log}_{10} L$ ($R^2 = 0.99$, $n = 223$).

Males: $\text{Log}_{10} M = -4.33 + 2.79 \text{Log}_{10} L$ ($R^2 = 0.99$, $n = 97$).

5.4 Discussion

5.4.1 Reproductive biology

The data presented in this chapter demonstrate that in Shark Bay *Carcharhinus cautus* copulates in late October–early November and ovulates and conceives in late November–early December, *i.e.* approximately four weeks later. This implies that sperm is stored in the oviducal gland for about four weeks until ovulation occurs, as is the case with certain other shark species, *e.g.* *C. tilstoni* (Stevens & Wiley, 1986) and *Prionace glauca* (Pratt, 1979). Since *C. cautus* subsequently gives birth in late October–early November, gestation lasts for approximately 11 months. Although the individuals of *C. cautus* in Darwin Harbour give birth at a similar time of the year as in Shark Bay, *i.e.* November, they ovulate at a different time, *i.e.* February and March *vs* late November–early December (Lyle, 1987). This species thus has a shorter gestation period in Darwin Harbour, *i.e.* 8–9 *vs* 11 months, which is presumably related to the warmer temperatures found in that environment, which is located at 12°30'S, *i.e.* *ca* 1460 km north of Shark Bay. The latter conclusion would be consistent with the observation that the gestation period of the clearnose skate *Raja*

eglanteria lasts for about three months in Delaware Bay, where water temperatures are 12–23°C, but for only two months in Florida where they are consistently above 24°C (Libby & Gilbert, 1960).

Mature non-pregnant females contained oocytes undergoing vitellogenesis for 12–13 months, *i.e.* from November or December to the beginning of the following December, and mature pregnant females contain embryos for 11 months, *i.e.* from December to October, demonstrating that *C. cautus* has a biennial reproductive cycle. This parallels the situation recorded for certain other carcharhinid sharks, *e.g.* the finetooth shark *Carcharhinus isodon* (Castro, 1993), the Galapagos shark *Carcharhinus galapagensis* (Wetherbee *et al.*, 1996) and the sandbar shark *Carcharhinus plumbeus* (Joung & Chen, 1995).

The estimated size at first maturity (L_{50}) and maximum size attained by *C. cautus* in Shark Bay were greater for females than males, *i.e.* 1007 and 1330 mm, respectively, vs 913 and 1110 mm, respectively. Although these trends parallel those recorded for *C. cautus* in Darwin Harbour, the above values are each approximately 100 mm greater than those recorded by Lyle (1987) in that more northern environment.

5.4.2 *Age composition and growth rates*

This present study demonstrated that, by the time they are born, the females and males of *Carcharhinus cautus* have attained *ca* 28 and 32%, respectively, of their lengths at their maximum observed age, as estimated from the Schnute growth equations for postnatal fish. The relatively large amount of growth undergone by this species prior to birth parallels the situation recorded for *Carcharhinus amblyrhynchos*, *C. brevipinna*, *C. falciformis*, *C. melanopterus* and *C. plumbeus*, amongst which their lengths at the time of parturition are between 25 and 38% of their maximum lengths (Lyle, 1987; Stevens & McLoughlin,

1991; Joung & Chen, 1995; Wetherbee *et al.*, 1997). It also parallels that recorded for the myliobatiforms *Urolophus lobatus*, *Trygonoptera personata* and *T. mucosa* (White *et al.*, 2001, 2002).

Almost every fishery paper concerned with growth uses the von Bertalanffy growth equation, even when it does not provide a particularly good fit (Haddon, 2001). Recent work on two species of rays belonging to the genus *Trygonoptera* showed that the Schnute growth equation produced a significantly better fit to the disc widths at age for these particular elasmobranchs than the von Bertalanffy growth equation (White *et al.*, 2002). During the present study of *C. cautus*, the use of the Schnute rather than von Bertalanffy growth equation significantly improved the fit for females during both postnatal life (Figs 5.5a vs 5.5c) and the whole of life (Figs 5.5e vs 5.5g) and of males during the whole of life (Figs 5.5f vs 5.5h), but not for males during postnatal life (Figs 5.5b vs 5.5d). Whenever possible, it is desirable to use the von Bertalanffy rather than the Schnute equation to describe growth in elasmobranchs, as it is both a simpler equation and the one that has almost invariably been used for this purpose with other members of this subclass (*e.g.* Branstetter, 1987b; Davenport & Stevens, 1988; Simpfendorfer, 1993; Simpfendorfer *et al.*, 2000) and which consequently facilitates comparisons with the estimates recorded for the von Bertalanffy growth parameters of other elasmobranch species. The fitting of an appropriate growth curve is important both for enabling a reliable estimate of the range of lengths of fish of a given age to be calculated and for yielding reliable parameters for the growth equation employed.

When a statistically significant difference is found between the curves produced by two different growth equations, it is important to recognise that the likelihood ratio test is extremely sensitive to small differences in these growth curves, when those curves have been fitted to a large number of size-at-age points, as is the situation both in my present

study and in that which was conducted on two *Trygonoptera* species (White *et al.*, 2002). The importance that has been placed on the von Bertalanffy growth parameters is exemplified by the fact that, for example, two of these parameters (k and L_{∞}) are used in the Pauly (1980a) equation for estimating the natural mortality of species. Thus, the poor values for these two parameters, which would result from a particularly bad fit at the bottom or top end of the curve, would generate poor estimates for natural mortality. The results of my analyses have thus been closely examined to see whether it would always be desirable to change from the von Bertalanffy to Schnute growth equations, when it significantly improved the fit from a statistical point of view but, from a biological perspective, might have limited relevance.

The coefficient of determination for the von Bertalanffy and Schnute growth curves for postnatal males of *C. cautus* were identical (0.953) and the quality of the fit was not significantly improved by using the more complex Schnute growth curve. There was thus no point in using the Schnute rather than the von Bertalanffy growth to describe the growth of postnatal males. However, the values for t_0 in the von Bertalanffy and Schnute growth equations for postnatal males, *i.e.* -21 and -17 months, respectively, exceeded the -11 months, that would be expected from the duration of gestation. This reflects, in part, the tendency for both curves to pass slightly above the points for the lengths-at-age of the youngest fish.

In contrast to the situation with postnatal males, the use of the Schnute rather than von Bertalanffy growth curve did improve significantly the quality of the fit to the length-at-age data for the males of *C. cautus* throughout life from conception. Yet, the coefficient of determination for the von Bertalanffy growth curve was still high (0.986) and only slightly less than that for the Schnute growth curve (0.991). In addition, the values for t_0 produced by both growth equations were very close to zero, as would ideally be expected

with these data, which employed the age of conception as age zero. The negligible values for t_0 reflect the excellent fit provided by both curves for the lengths-at-age of the youngest fish, *i.e.* those during the early part of embryonic life. Moreover, the L_∞ s differed by only 65 mm and the maximum difference between the curves at any point after age 1 was only 4.5%. Thus, although the Schnute growth curve did improve the fit to the length-at-age data for particularly the older fish, the value of using this growth curve rather than the von Bertalanffy growth curve for describing the growth of males throughout life is considered to be limited.

The coefficient of determination for the von Bertalanffy growth equation for female *C. cautilus* during just postnatal life was 0.892, reflecting the reasonably good fit of the curve to the length-at-age data. However, visual comparisons between Figs 5.5a and 5.5c show that the Schnute growth curve provides a better fit to particularly the lengths at age at the extreme ends of the curves, these differences being reflected in a higher coefficient of determination (0.919), a less negative t_0 and a greater L_∞ and the significant difference between the curves. The shift in the L_∞ was particularly marked, with this parameter increasing from 1242 to 2238 mm. Moreover, the maximum difference between the curves reached 5%. Thus, although the von Bertalanffy growth curves provided a good fit to most of the data, there would be an advantage in using the Schnute growth curve if an accurate estimate of the age of a young or old female of given length was required.

The use of the Schnute growth curve rather than the von Bertalanffy growth curve to describe the growth of females throughout life also resulted in an upwards shift at the upper end to help accommodate the location of the lengths of the older individuals. This resulted in an increase in the L_∞ from 1161 to 1308 mm. Furthermore, the maximum difference between the lengths of fish derived from the curves was 6.0%. Thus, although

the coefficient of determination was high for the von Bertalanffy growth curves throughout the whole of life (0.976), there would be value in using the Schnute curve ($R^2 = 0.983$) for estimating the likely age of the older fish from their lengths.

The k values for postnatal male and female *C. cautilus*, 0.287 and 0.190 year⁻¹, respectively, lie towards the upper end of the range for elasmobranchs, as would be expected for this small to medium-sized shark (Frisk *et al.*, 2001). In the context of asymptotic length, it has been proposed that a value equivalent to about $L_{\max}/0.95$ would be expected (*e.g.* Pauly, 1980b). More recently, Froese & Binohlan (2000) have used data for a large number of species to develop an empirical relationship between the von Bertalanffy L_{∞} and L_{\max} which, in the case of the data for male and female *C. cautilus*, would be represented by $L_{\infty} \approx L_{\max}/0.97$. The latter relationship yields estimates for L_{∞} of 1140 mm for males and 1362 mm for females. The L_{∞} s derived for males during postnatal life using the von Bertalanffy growth equation, 1105 mm, and the Schnute growth equation, 1129 mm, and for the whole of life using the Schnute equation, 1098 mm, were all close to the above “hypothetical” L_{∞} , whereas the L_{∞} for males derived for the whole of life using the von Bertalanffy growth equation, 1033 mm was slightly below that “hypothetical” L_{∞} . The L_{∞} derived for females during the whole of life using the Schnute growth equation, 1308 mm, was closer to the “hypothetical” L_{∞} of 1362 mm for that sex than the L_{∞} s of 1242 mm, and even more particularly the 1161 mm, that were both derived employing the von Bertalanffy growth equation for females during postnatal life and the whole of life, respectively. However, the L_{∞} of 2238 mm derived for females during postnatal life using the Schnute equation far exceeded that “hypothetical” L_{∞} for females. The Schnute growth equation for postnatal females produced such a high L_{∞} through accommodating the lengths-at-age of the older fish, thus emphasising the problems posed by always having a

fixed concept as to what constitutes an appropriate value for L_{∞} . The derivation of a L_{∞} for females during postnatal life using the von Bertalanffy growth curve that was appreciably lower than the above “hypothetical” L_{∞} emphasises that difficulties with predicting the L_{∞} on the basis of an empirical equation are not just restricted to the use of the Schnute growth equation. The significance of the L_{∞} s derived from growth equations thus has to be interpreted with great caution (see also Knight, 1968).

Through their addition of a fifth parameter, Schnute & Richards (1990) extended the generalization of the curve produced by Schnute (1981). Although the use of the Schnute and Richards curve significantly improved the fit to the lengths-at-age for both males ($P < 0.01$) and females from conception ($P < 0.001$) (but not for either sex from parturition), the maximum difference between the lengths estimated for any points in the growth curves in either of those first two cases was less than 3%. Thus, even in these cases, a shift to the more complex growth equation would be of limited value.

I consider that, during this study, the use of the maximum differences at any point along the lines of the two growth curves, in conjunction with statistical tests and comparisons between the values for the coefficient of determination, t_0 and L_{∞} , has reduced the subjectivity in assessing when it is appropriate to consider using more complex growth curves, such as those of Schnute (1981) and of Schnute & Richards (1990). The growth curves constructed using the lengths-at-age of female and male *C. cautilus* during pre- and postnatal life demonstrated that, even though there was a huge shift at birth from obtaining food internally via a placenta to having to forage actively for prey, parturition was not accompanied by an abrupt change in the pattern of growth. Thus, in those cases where there is a shortage of length-at-age data for a shark species in the period immediately following birth, the inclusion of lengths-at-age of individuals during embryonic life would be likely to

increase the quality of the curve representing the growth of fish during postnatal life. The ability to use a smooth, monotonically increasing growth equation to describe the pattern of increase in length-at-age of *C. cautus* throughout the whole of life and thus commencing at the onset of embryonic growth parallels the situation recorded using the disc widths-at-age of two species belonging to the Myliobatiformes, a morphologically very different suborder of elasmobranchs (White *et al.*, 2002).

CHAPTER 6

Species and size compositions of chondrichthyans in target and non-target fisheries of south-eastern Indonesia

6.1 Introduction

Indonesia has one of the richest elasmobranch faunas and the largest chondrichthyan fishery in the world, with an estimated 87 138 and 100 000 tonnes landed in 1993 and 1996, respectively (Bonfil, 1994; Monintja & Poernomo, 2000; Widodo, 2000). However, there are almost no data on the species or size composition of these landings. The only information available on the catches of individual species is that provided by pelagic tuna fishers, who estimated that, in 1999, they landed 5 217 tonnes of mako sharks (*Isurus paucus* and *I. oxyrinchus*) and 47 079 tonnes of other species (Priyono, 2000). The catches and fishing effort for elasmobranchs are increasing and the catch per unit effort (CPUE) is decreasing (Monintja & Poernomo, 2000), which suggests that the overall abundance of these cartilaginous fishes is declining. The high diversity of the elasmobranch fauna in Indonesia has been well documented by Gloerfelt-Tarp & Kailola (1984), Last & Stevens (1994) and Carpenter & Niem (1998, 1999). These authors highlighted the need for research in certain areas and, in particular, the acquisition of sound taxonomic data so that the various species could be reliably identified and reliable data could be obtained for the geographical distribution and biology of many of the species.

Elasmobranchs are caught in Indonesia by both target fisheries and as bycatch in other fisheries. Target fisheries, which are mainly artisanal, use a variety of fishing methods, such as gillnets, trammel nets, purse seines, longlines and droplines. The fisheries that land substantial catches of elasmobranchs as a bycatch include the prawn and fish fishery exploited by commercial trawlers and pelagic tuna fisheries. All of the body parts of the elasmobranchs landed are utilised. The flesh, which is often dried, is used for local consumption, whereas the fins, and particularly those of carcharhinid sharks, are dried and exported to other Asian countries where they are highly valued (Chen, 1996). The skins of dasyatid rays are often dried and used by specialist manufacturers to produce wallets,

purses, belts and other commodities (WT White, pers. obs.). Squalene oil from the livers of some shark species (mainly squaloids) is also commonly exported. Indeed, several companies in Indonesia export as much as 48 000 kg of liver oil annually (Chen, 1996). Other exported shark products include the dried cartilage of larger individuals and there is a growing demand for specialist products at particular locations, such as the gill rakers of mobulid rays (WT White, pers. obs.). Shark and ray products that are utilised locally include not only dried shark and ray flesh (as food), but also dried ray tails (used commonly as horse whips), shark jaws (sales to tourists) and fresh squalid oocytes (as a delicacy in some areas) (WT White, pers. obs.).

The main aim of this study was to provide the first detailed assessment of the compositions and relative abundances of species of chondrichthyans in the target and non-target fisheries of eastern Indonesia (see Appendix I for species accounts). Focus has also been placed on recording the fishing gear used and the extent to which chondrichthyans are targeted within these fisheries. The degree to which the composition of chondrichthyan species varies between both landing sites and fishing method has also been explored. The size compositions of the most abundant species and the size at maturity of the males were also determined using the extent to which their claspers were calcified as a criterion for maturity. The lengths of the claspers were plotted against surrogates for body size, *i.e.* length or disc width, for each of the most abundant species to ascertain over what range in body size the claspers underwent a rapid relative enlargement in size and then became fully calcified. Biological data for three of the most abundant dasyatid species are presented in Appendix II. The final aim was to determine which chondrichthyan species had not been described and thus require taxonomic studies.

6.2 Methods

6.2.1 Survey regime

The location and a description of the landing sites surveyed in eastern Indonesia are given in Chapter 2, and the months that each of these sites were sampled are recorded in Table 6.1. On each sampling trip, the major landing sites were generally visited on two or three occasions at around their peak operating time, which ranged from 0600 h at Tanjung Luar to 0900 h at Muara Angke.

Table 6.1 Number of occasions each landing site was sampled on each of the nine trips to Indonesia.

Region	Landing site	2001					2002			2003
		April	July	Nov	March	May	June	Aug	Oct	Feb
Java	Muara Angke	3	3	-	4	4	-	4	-	5
	Muara Baru	-	1	-	3	-	-	1	-	2
	Palabuhanratu	1	1	-	2	2	-	1	-	2
	Cilacap	2	2	-	2	-	2	1	-	-
	Pekalongan	1	-	-	-	-	-	-	-	-
Bali	Kedonganan	1	4	2	4	-	8	4	5	4
Lombok	Tanjung Luar	2	2	1	2	-	3	2	1	-
West Timor	Kupang	-	-	-	-	-	2	-	-	-
Sulawesi	Kendari	2	-	-	-	-	-	-	-	-
Papua	Merauke	-	-	-	-	-	-	-	5	-

6.2.2 Survey techniques

The landing site surveys were undertaken in collaboration with two fisheries research scientists from two collaborating organisations in Indonesia, *i.e.* the Research Institute for Marine Fisheries (RIMF) and the Indonesian Institute of Sciences (LIPI), and a socioeconomist from the Centre for Agricultural and Socioeconomic Research (CASER). Since, after unloading their catch, the fishers at each landing site either process this catch or transport it to a processing–packaging area within one to three hours, the biological data

that could be recorded on each occasion ultimately depended on the amount of time available for “examining” the fish on that particular occasion.

On arriving at a landing site, the initial focus was concentrated on determining which chondrichthyan species were present in the landings present on that day. The species were identified using the keys and/or illustrations in Carpenter & Niem (1998, 1999), Compagno (1984), Last & Stevens (1994) and Sainsbury *et al.* (1985). However, when a species was not recorded in the above keys, it was assigned to its appropriate genus and provided with an appropriate temporary name. Whenever possible, those species that could not be accurately identified using the above references were purchased and stored in plastic holding tanks containing 10% formalin for subsequent identification.

The numbers and biomass (kg) of each species at each landing site on each sampling occasion were recorded. The numbers of each species represent actual counts, except when the numbers of a species were large, in which case the numbers represent visual estimates. The collective mass of each species was always estimated visually using a combination of the number of that species and the typical masses of individuals of morphologically similar taxa of comparable size. Whenever possible, the sex and size (length in sharks, holocephalans, shovelnose rays and guitarfishes, and disc width in all other rays) of the individuals of each species were recorded to the nearest 1 mm. In the case of males, the length of the claspers, from insertion of pelvic fin to tip of the clasper (to the nearest 1 mm), and level of calcification, *i.e.* non-calcified, not fully calcified or fully calcified, were also recorded whenever possible. The information that was also collected from the fishers included gear characteristics and the duration and location of each fishing trip.

6.2.3 Data analyses

The percentage compositions of each species at each landing site on each sampling occasion were ordinated using the non-metric multidimensional scaling techniques in the PRIMER v5.2.2 package (Clarke & Gorley 2001). Prior to ordination, the percentage compositions were square root transformed, and a similarity matrix constructed using the Bray-Curtis similarity coefficient. One-way analysis of similarities (ANOSIM) was employed to test whether the species compositions in the samples from each landing site on each occasion were significantly different (Clarke 1993). Multivariate dispersion (MVDISP) was used to determine the extent to which the points representing the samples in each *a priori* group were dispersed (Sommerfield & Clarke, 1997) and similarity percentages (SIMPER) were used to determine which species typified each site (Clarke, 1993). The groups of “samples” formed by the above ordination appeared to reflect the main fishing methods employed at those locations, *e.g.* gillnetting for dasyatids and rhynchobatids at Muara Angke, Benoa Harbour and Merauke. Thus, a further ordination was carried out using separately the percentage species composition data for each fishing method on each sampling occasion throughout the sampling period.

The size at maturity of males was calculated for those species for which there were sufficient data on clasper length and calcification of a wide size range of individuals. Those individuals with claspers that were either non-calcified or not fully calcified were considered immature and those with fully calcified claspers were considered mature. The length or disc width, at which 50% of males of each species attain maturity (*i.e.* the L_{50} or DW_{50} at maturity) was derived by logistic regression, where the proportion, p_S , of those sharks or rays that were mature at size S was calculated as,

$$p_s = \frac{1}{1 + \exp\left[-\ln(19)\frac{(S - S_{50})}{(S_{95} - S_{50})}\right]},$$

and where S_{50} and S_{95} are constants and \ln is the natural logarithm. Maximum likelihood estimates of the parameters were obtained using the routine SOLVER in Microsoft™ Excel and calculating the likelihood of immature and mature individuals as $1 - p_s$ and p_s , respectively. The reported estimates of the parameters were determined as the median values derived from 200 sets of randomly-resampled data, with the same sample size, drawn from the data on observed maturity status at size for male sharks or rays. The approximate 95% confidence intervals were estimated as the 2.5 and 97.5 percentiles of the 200 estimates resulting from these resampled data.

The relationships between the clasper lengths (CL) of the males of the most abundant species and their corresponding body sizes (S , either total length or disc width) were described using the modified logistic function,

$$CL = \text{base} + \frac{\text{max}}{1 + \exp\left[-\ln(19)\frac{(S - a)}{(b - a)}\right]},$$

where a and b are parameters that determine the shape of this relationship. This function ranges from the lower limit of base, when S is small, to an upper limit of base + max when S is large and attains a midpoint between these extremes when $S = a$ and a value that is base + 95% of the distance between the extremes when $S = b$. The parameter a will subsequently be termed the “size at inflection”. The regression was fitted using the nonlinear procedure in SPSS (SPSS inc., 1999).

6.3 Results

6.3.1 Overall species composition

A total of 19 573 chondrichthyan fishes, representing 139 species and 29 families, was recorded collectively at the landing sites in south-eastern Indonesia between April 2001 and February 2003. This total comprised 77 species of shark representing 17 families and 61 species of ray representing 11 families and a single species of holocephalan (Table 6.2; see Appendix I for species accounts). The most speciose and commonly recorded families were the Dasyatidae and Carcharhinidae, which were represented by 30 and 25 species, respectively, and contributed 65.2 and 19.6%, respectively, to the total number of individuals of all species (see Table 6.2). The most abundant dasyatids were *Dasyatis kuhlii*, *Dasyatis zugei*, *Himantura walga* and *Himantura* sp. sparse spot (*cf. gerrardi*), which collectively comprised 57.8% of the total number of all chondrichthyans.

Preliminary data on the biology of three of the above dasyatids, *i.e.* *D. kuhlii*, *D. zugei* and *H. walga*, are presented in Appendix II. The most abundant carcharhinid species were *Scoliodon laticaudus*, *Rhizoprionodon oligolinx*, *Carcharhinus falciformis* and *C. sorrah*, which together comprised 14.2% of the total number of chondrichthyans caught. The above two families also made the greatest contribution to the total estimated biomass of chondrichthyans, *i.e.* 36.6 and 23.3%, respectively, amongst which *Himantura fai*, *Pastinachus sephen*, *Dasyatis kuhlii*, *Prionace glauca* and *Carcharhinus falciformis* were the greatest contributors. However, the collective contribution of *Rhynchobatus cf. australiae*, *Alopias pelagicus* and *Manta birostris* to the total biomass was also substantial, *i.e.* 18.7%.

6.3.2 *Species compositions between landing sites*

The number of species recorded at the landing sites was greatest at Kedonganan and Tanjung Luar, *i.e.* 79 and 72, respectively, which were predominantly sharks, and were least at Kendari and Kupang, *i.e.* 5 and 4, respectively (Fig. 6.1). Although fewer species were recorded at Muara Angke, *i.e.* 52, than at the first two landing sites, this site yielded the greatest number of ray species.

Following ordination of the percentage contributions of each species in the samples from each of the eight main landing sites, the points representing each of those sites tended to occupy a particular part of the ordination plot (Fig. 6.2). The points for Muara Angke formed a particularly tight and discrete group in the left of the plot and to the right and below those for Bena Harbour and Merauke and to the left of those for Muara Baru. The points for Palabuhanratu and Cilacap intermingled in the lower right of the plot, just below a tight group comprising the samples from Tanjung Luar (Fig. 6.2). All but one of the samples from Kedonganan lay above and/or to the left of that latter group. A one-way ANOSIM showed that the species compositions at the six locations for which there were at least four samples, *i.e.* excluding Merauke and Bena Harbour, were significantly different ($P < 0.001$; R statistic = 0.765), and that all pairwise comparisons differed significantly ($P < 0.05$). A one-way ANOSIM showed that the species compositions did not differ significantly among months ($P > 0.05$; R statistic = -0.032) or in any of the pairwise comparisons between months. The samples from the sites for which there were four or more samples, except for Muara Angke, were widely dispersed. This is reflected in the high dispersion values for these sites, which ranged from 0.976 to 1.393, compared with the low value for Muara Angke, *i.e.* 0.255. Those species shown by SIMPER to typify each of the landing sites are shown in Table 6.3.

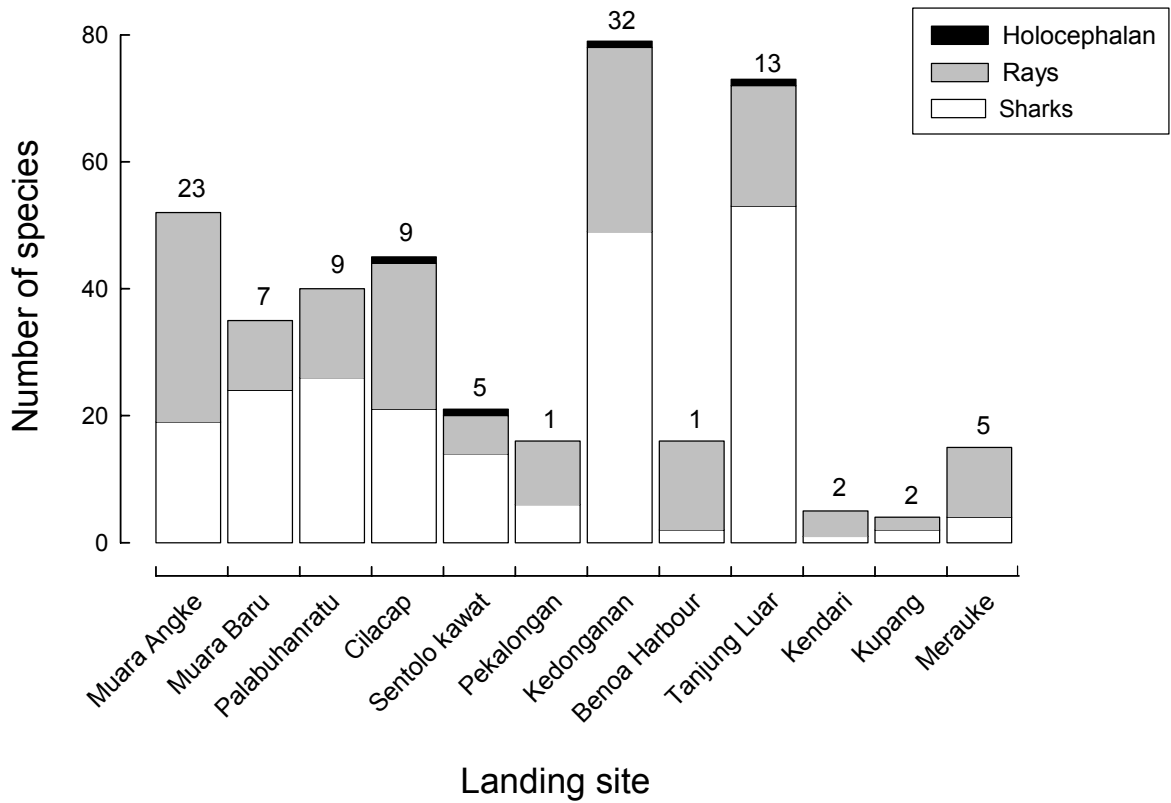


Figure 6.1 Numbers of species of sharks, rays and holocephalans recorded at each landing site and the numbers of visits (above bars) to each of those landing sites.

Landing sites

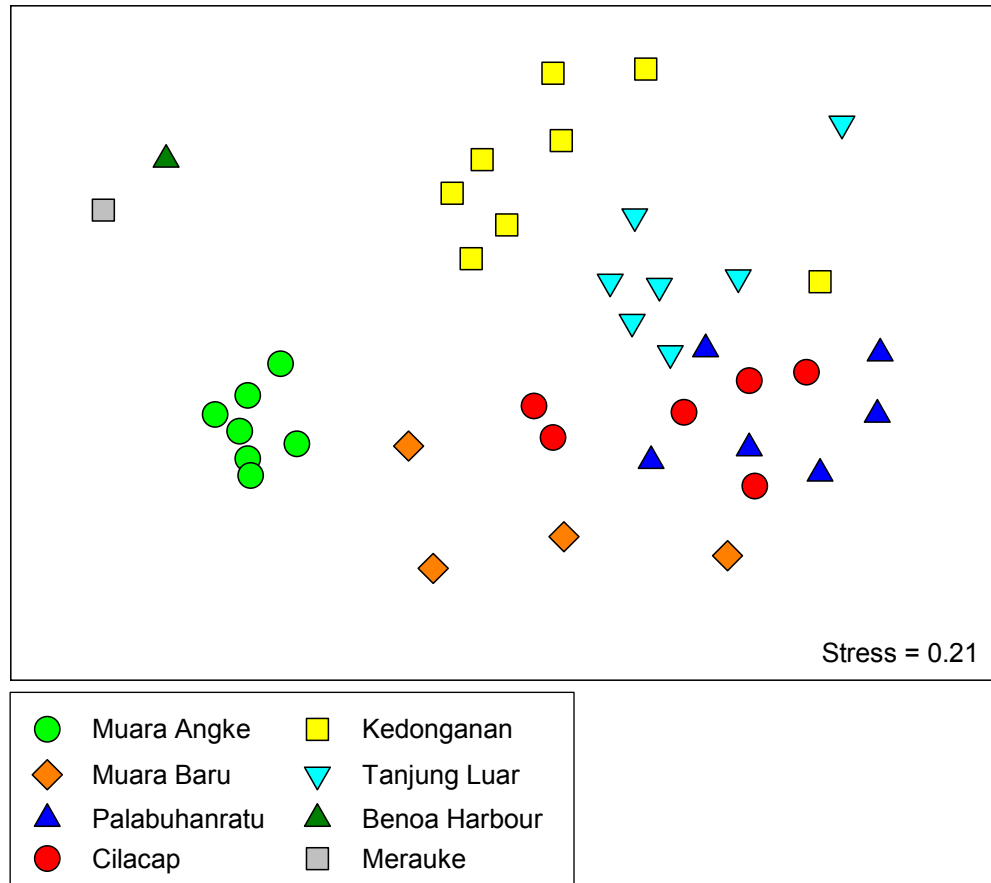


Figure 6.2 Non-metric multidimensional scaling ordination of the percentage contributions of each chondrichthyan in the samples from each of the main landings sites on each sampling occasion.

Table 6.3 Species shown by SIMPER to typify each of the main landing sites in south-eastern Indonesia.

Landing sites			
Muara Angke	<i>Dasyatis kuhlii</i>	<i>Dasyatis zugei</i>	
Muara Baru	<i>Carcharhinus sorrah</i>	<i>Carcharhinus dussumieri</i>	
Palabuhanratu	<i>Carcharhinus falciformis</i>	<i>Mobula japonica</i>	
Cilacap	<i>Carcharhinus falciformis</i>	<i>Alopias pelagicus</i>	
Kedonganan	<i>Squalus</i> sp. 3b	<i>Rhinobatus</i> sp. 1	<i>Aetoplatea zonura</i>
Tanjung Luar	<i>Carcharhinus falciformis</i>	<i>Carcharhinus amblyrhynchos</i>	

6.3.3 Target fisheries for elasmobranchs

The characteristics of the gear utilised, depth fished, trip duration and fishing locations of each of the fishing methods are shown in Table 6.4.

Demersal gillnet fishery for dasyatid and rhynchobatid rays

The operation of the demersal gillnet fisheries for dasyatid and rhynchobatids was observed from the landing sites of Muara Angke, Bena Harbour and Merauke. The nets used by these fishers, which are 5000 to 6000 m in length and have a large mesh (500 mm), are hung very loosely and designed to entangle the large dasyatid and rhynchobatid rays (see Table 6.4). At both Bena Harbour and Merauke, this fishery comprised only one boat, which operates in both the Banda and Arafura Seas (see Fig. 2.2; Table 6.4). The catches are frozen onboard immediately after capture and are then shipped or trucked to a specialised processing area at Muara Angke in Jakarta. A large fleet (>50 boats) operates out of the landing site of Muara Angke, with their fishing grounds being located in the Java Sea and off West Sumatra. The rays are stored on a minimal amount of ice for 50–60 days and are thus landed in poor condition. The total catch from each boat, which can exceed 30 tonnes, is transferred to the specialised processing area. The rays are skinned and the

flesh cut into very thin pieces that are placed in brine tanks (Plates 6.1, 6.2) and the salted flesh later placed on a bamboo drying rack. The skins and cartilage are dried (Plates 6.3, 6.4). The dried flesh is packaged for either export or local consumption, whereas the skins are sold to specialised manufacturers, *e.g.* in Thailand and Cilacap, who use them to produce wallets, hand bags, belts, shoes, etc. The cartilage is usually exported, either whole or in powdered form, to the oriental market for its purported medicinal properties.

A total of 34 species was recorded in the catches of this demersal gillnet fishery, the majority of which, *i.e.* 28, were rays. The most abundant species were *Rhynchobatus cf. australiae*, *Himantura* sp. sparse spot (*cf. gerrardi*), *Himantura fai* and *Pastinachus sephen* (Fig. 6.3a). Another abundant species, *Himantura jenkinsii*, has a greater value than the other dasyatids due to its possession of enlarged thorn-like denticles on the dorsal midline and tail that make the skins ideal for the production of belts.

Demersal gillnet fishery for small rays

A demersal gillnet fishery targeting small rays was observed operating out of the landing site of Kedonganan in Bali. The gillnets, which are *ca* 1200 m in length with 100 mm mesh, are deployed from a number of small boats (<10 m in length) that operate in relatively shallow water, *i.e.* <30 m, in Jimbaran Bay (Table 6.4). These boats only remain at sea for one or two nights and typically land less than a hundred small-medium rays on each occasion. The flesh of all of the rays landed are utilised locally for human consumption. A total of 16 species was recorded from this fishery at Kedonganan, with *Rhinobatus* sp. 1 and *Dasyatis kuhlii* (Bali form) constituting more than 60% of the catches (Fig. 6.3b).

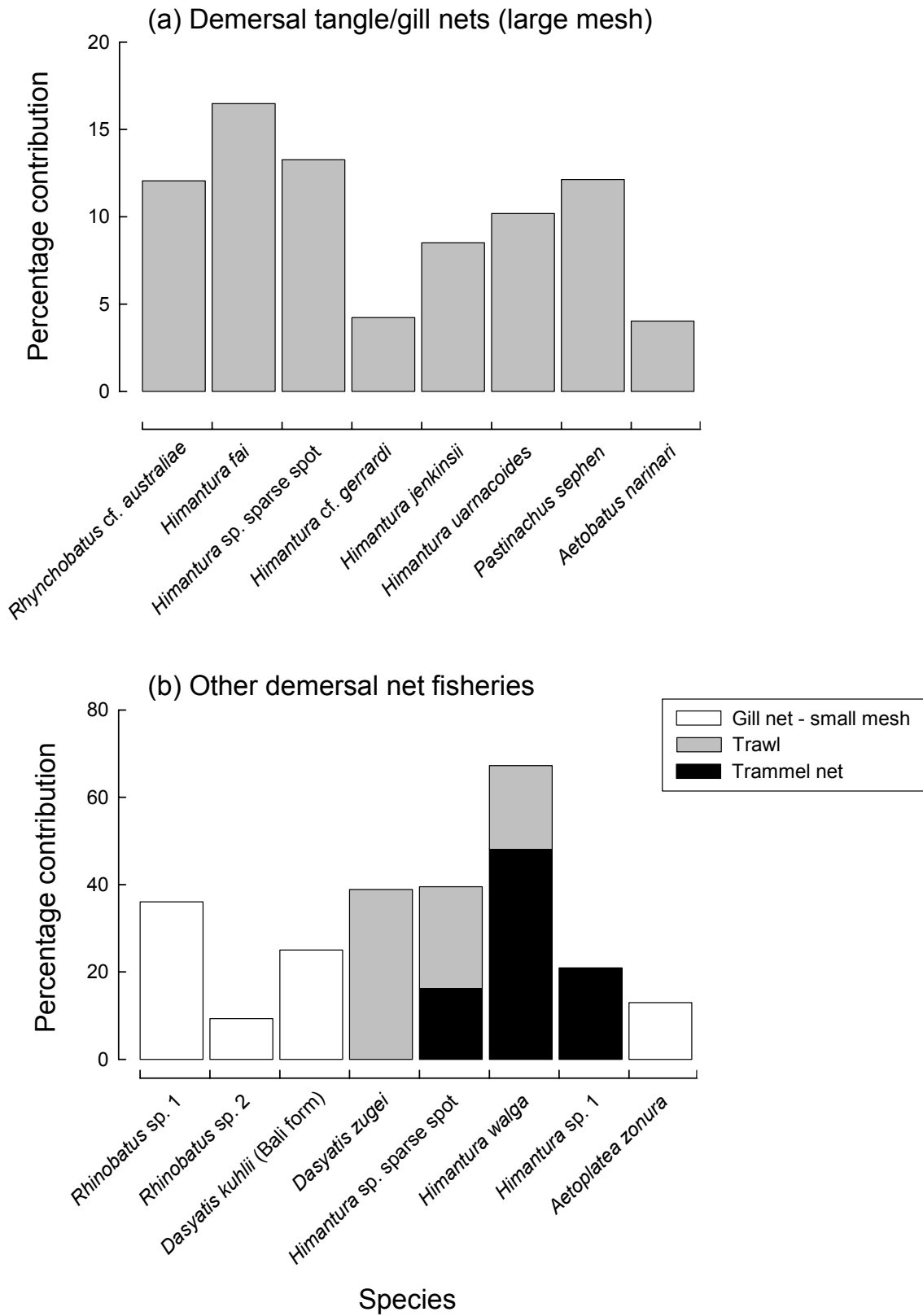


Figure 6.3 Percentage contributions of the most abundant species by numbers to (a) the demersal tangle–gillnet fishery and (b) the other demersal net fisheries in south-eastern Indonesia.

Pelagic longline fisheries for carcharhinids

Pelagic longline fisheries targeting large carcharhinid sharks were observed operating out of the landing sites of Palabuhanratu and Tanjung Luar. The longlines, which range in length from 3000 to 5000 m, each contain between 400 and 600 hooks (Table 6.4). The longliners from Palabuhanratu operate in oceanic waters off West Sumatra as well as southwards towards Australian waters. At Tanjung Luar, the longliners operate in both oceanic and inshore waters off south Flores, Sumbawa and further south to Sumba. At both sites, the number of boats in this fishery is relatively large, *e.g.* >50 at Tanjung Luar, and the boats remain at sea for 7–15 days. All sharks landed in this fishery at these two sites are typically landed whole, *i.e.* not finned and/or trunked. The total catch at Tanjung Luar from several of these longline boats on one day in the peak season can constitute as much as 60% of the total biomass of all catches, *i.e.* including teleosts, cephalopods etc. The fins are taken away for drying and supplied to the oriental shark-fin trade which pay high prices for this product and the flesh is also used either fresh, smoked or salted and dried for human consumption. A total of 21 species of shark was recorded from this fishery at these two sites. The most abundant species caught in this fishery were *Alopias pelagicus*, *Carcharhinus amblyrhynchos*, *C. falciformis*, *Prionace glauca* and *Sphyrna lewini* (Fig. 6.4a).

Demersal longline fishery for squaloids

Demersal longline fisheries that target mainly squaloids were observed operating out of the landing sites of Palabuhanratu, Cilacap (Sentolo kawat), Kedonganan and Tanjung Luar. The longlines used by these fisheries vary between landing sites, with only small longlines, *i.e.* ca 200 m in length, being used at Kedonganan and larger lines, *i.e.* >2000 m in length, being employed at Palabuhanratu and Tanjung Luar (Table 6.4). The catches from this

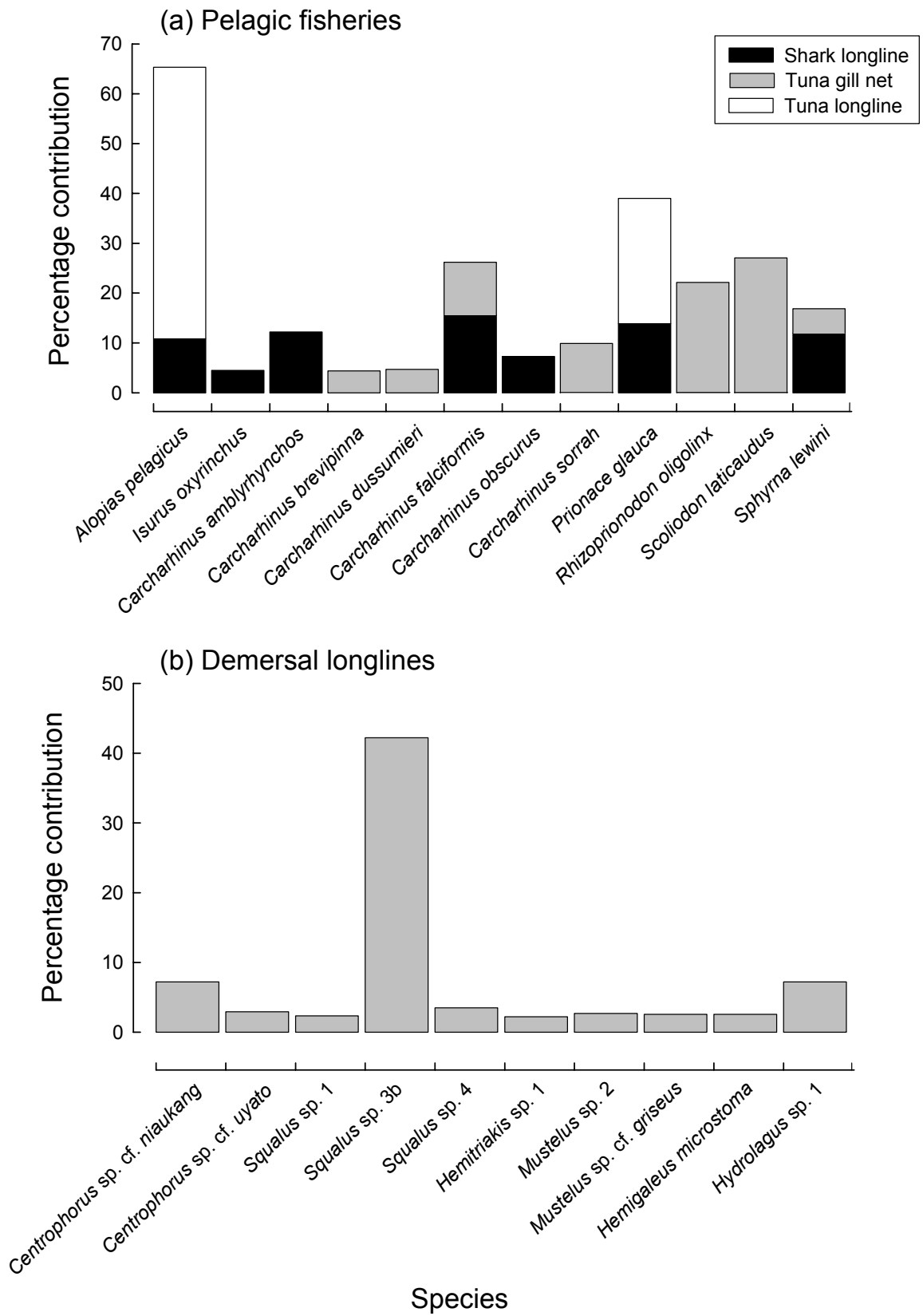


Figure 6.4 Percentage contributions of the most abundant species by numbers to (a) the pelagic fisheries and (b) the demersal longline fishery in south-eastern Indonesia.

fishery at most sites appear to be highly seasonal. The livers of the squaloid sharks are excised immediately upon landing and the squalene oil, which has a high export value, subsequently extracted. The livers of the large deep-water centrophorids, namely *Centrophorus* sp. cf. *niaukang* and *C. sp. cf. squamosus*, are the most sought after as they possess extremely large livers with high squalene levels. The fins and vertebrae are dried for either export or local use and the flesh is salted and dried for human consumption (Plates 6.5, 6.6). Furthermore, at the landing site of Palabuhanratu, the very large, mature oocytes of the above centrophorids species, which can exceed 50 mm in diameter, are also considered a local delicacy.

A total of 35 species, *i.e.* 3 ray species, 31 shark species and 1 species of holocephalan, were recorded from this fishery in south-eastern Indonesia. However, the total number of species recorded in this fishery varied greatly between sites, with only seven species being recorded at Palabuhanratu and Cilacap (Sentolo Kawat) compared with 27 at Kedonganan. The most abundant species, *i.e.* *Squalus* sp. 3b, constituted 42% of the total landings of this fishery, with *Centrophorus* sp. cf. *niaukang* and *Hydrolagus* sp. 1 both contributing 7.2% to the total numbers landed (Fig. 6.4b).

6.3.4 *Non-target fisheries for elasmobranchs*

Gillnet fishery for tuna

Gillnet fisheries for tuna were observed operating out of the landing sites of Muara Baru, Palabuhanratu, Cilacap, Kedonganan and Tanjung Luar. Although the main target species of these fisheries is the skipjack tuna *Katsuwonus pelamis*, substantial numbers of various other scombrids and istiophorids are also caught. The lengths of the nets vary between sites, with the gillnets at Tanjung Luar, which were approximately 800 m in length, being relatively smaller than those at Cilacap, *i.e.* up to 3000 m in length (Table 6.4). Although

scombrids constituted the largest proportion of the total landings from this fishery, elasmobranchs also made a significant contribution to these catches. At the landing site of Palabuhanratu, a number of such gillnetting boats are also involved in the target shark longline fishery. If weather permits, the boats move further out to sea where the tuna caught by the gillnets are used as bait for the longlines.

A total of 31 species, comprising seven species of ray and 24 species of shark, were recorded in this fishery, the most abundant of which were *Carcharhinus falciformis*, *C. sorrah*, *Rhizoprionodon oligolinx* and *Scoliodon laticaudus* (Fig. 6.4a). However, although the latter two species were the most abundant, they are very small, *i.e.* <700 mm TL, and make only a small contribution to the total biomass of the catches of this fishery. Furthermore, these two species were only observed at the landing site of Muara Baru, reflecting that they were caught in a more inshore fishery using smaller mesh gillnets. Although carcharhinids were also the most abundant elasmobranchs at the landing sites of Palabuhanratu, Cilacap and Tanjung Luar, members of the Mobulidae, and predominantly *Mobula japonica* and *M. tarapacana*, made, due to their large size (more than 3 m DW), a far greater contribution to the biomass of elasmobranchs. The gill rakers from these *Mobula* rays attract a high export value and are excised and retained fresh immediately after landing.

Pelagic longline fishery for tuna

Large-scale pelagic longline fisheries for tuna were observed operating out of the landing sites of Muara Baru and Cilacap. Although the size of the longlines used by longliners at Muara Baru was not known, the longlines used at Cilacap were approximately 20 000 m in length and contained approximately 2000 hooks (Table 6.4). Sharks only represented a small proportion of the total catches in this fishery, however, one boat sometimes lands up

to 40 large (2–3 m) members of the *Alopias* genus. Although a large proportion of the tuna longlining fleet at both sites do not land any whole sharks, they do retain the fins of all sharks caught. This is particularly the case with the largest of the boats operating in this fishery, which target yellowfin and bluefin tuna, whereas many of the smaller boats typically land whole sharks. The sharks are sent to small processing areas where the fins and cartilage are dried and the flesh is salted and then dried on bamboo drying racks. The skins from the trunks of adult *Prionace glauca* are also dried and used as food in some regions. A total of 11 species were recorded with *Alopias pelagicus* and *Prionace glauca* constituting 80% of the total numbers landed by this fishery (Fig. 6.4a).

Trammel net fishery for penaeid prawns and teleosts

A trammel net fishery for penaeids and/or teleosts was observed at the landing sites of Palabuhanratu and Cilacap. The small number of trammel net fishing boats observed at Palabuhanratu operate in inshore waters in depths of 30–40 m (Table 6.4). The only elasmobranchs observed in the catches obtained by these boats were *Himantura walga* and *H. sp. sparse spot* (cf. *gerrardi*) and these were present only in very low numbers. A large number of small-medium sized boats were observed operating trammel nets at the landing site of Cilacap. These boats employed longer nets, *i.e.* 60–120 m in length, and fished in deeper waters (Table 6.4). The target species were penaeid prawns, but a large number of small teleosts, predominantly sciaenids and polynemids, were also landed. In contrast, only a very small proportion of the landings of this fishery were elasmobranchs. A total of nine species were recorded from this fishery, with *Himantura walga*, *H. sp. 1* and *H. sp. sparse spot* (cf. *gerrardi*) being the most abundant (Fig. 6.3b).

Trawling for prawns and teleosts

Trawl fisheries were observed operating out of the ports of Muara Angke and Merauke. The substantial number of trawlers that operate in the Java Sea out of the former landing site target mainly penaeid prawns (see Table 6.4). Although elasmobranchs constitute only a minor proportion of the overall catch, large numbers of small rays, *i.e.* predominantly *Dasyatis zugei*, *Himantura walga* and *H. sp. sparse spot (cf. gerrardi)*, are typically landed by each trawler. A total of 18 species were recorded in this fishery at Muara Angke, with the above three species collectively constituting 81% to the total numbers landed (Fig. 6.3b).

The trawl fishery at Merauke is very large, consisting of more than 600 boats (mostly Thai owned and operated), each with the capability of storing a catch exceeding 200 tonnes. The boats unload their catches directly into the export “mother” ships, a process which can take several nights, and these catches are then immediately exported overseas. Due to this method of unloading, and since Merauke was surveyed on only one occasion, the catches could only be observed for several hours and thus a comprehensive assessment of the species compositions of elasmobranchs in this fishery could not be undertaken. These trawlers operate in the Arafura and Banda Seas and target teleosts in their demersal trawling practices. Only ten elasmobranch species were observed with *Rhizoprionodon taylori*, *Himantura toshi* and *H. fai* being the most abundant species. No small rays were caught due to the large mesh used by these trawlers.

Seine netting for penaeid prawns

A small and localised seine net fishery for penaeid prawns was observed operating from the shore at beach villages situated along the coast of Merauke in Papua. The seine nets are approximately 40 m in length and are operated for several hours in shallow (waist-deep)

waters along the beaches on a low but rising tide. In terms of mass, the catches in each seine net consisted of approximately 40–50% penaeid prawns, 50–55% teleosts (predominantly sciaenids and polynemids) and 0–5% elasmobranchs. The fishers operate the nets about 100–150 mm from the substrate surface to avoid catching rays, which are abundant in the nearshore, shallow waters in this region. Such rays have a low market value, especially when compared with penaeids, and the capture of a particularly large ray would require the fishers to stop seining until it could be removed. Five species of rays were observed in the seine net, with *Dasyatis* sp. 3 and *Himantura* sp. 2 being the most abundant.

Trapping for teleosts

A fish trap fishery was observed at Muara Angke that primarily targets lutjanids, but also catches a large variety of other reef-dwelling teleost species (Table 6.4). Although constituting only a minor part of the total catches, a single elasmobranch species, *i.e.* *Dasyatis kuhlii* (Java form), was caught in substantial numbers by the majority of boats operating in this fishery.

Other minor fisheries

Elasmobranchs were also observed in the catches of various small-scale fisheries, including handlining and droplining, at various landing sites. However, these fishers usually only operate opportunistically and only land small numbers of elasmobranchs.

6.3.5 *Ordination of species compositions of the different fishing methods*

Following ordination of the percentage compositions of the various species caught by each of the fishing methods on each sampling occasion, the points for the samples obtained by

each of these methods tended to form relatively tight groups on the ordination plot (Fig. 6.5). The points for fish trapping formed a tight and discrete grouping in the extreme upper left part of the plot, immediately to the left and/or above those for demersal longlining (Fig. 6.5). The points for tuna and target pelagic (shark) longlining were intermingled on the far right of the plot and just below and to the right of those for tuna gillnetting. The points for the samples obtained using all remaining methods (except seine nets which was represented by only one point that was located in the lowest and central portion of the plot) each formed discrete groups in the left of the plot (Fig. 6.5). A one-way ANOSIM showed that the species compositions in the catches obtained by the different fishing methods were significantly different ($P < 0.001$; R statistic = 0.850), and the same was true for all pairwise comparisons ($P < 0.01$ – 0.001 ; R statistic = 0.386–0.982). Note that seine netting was not included in this and subsequent analyses because this fishing method was represented by only one sample. A one-way ANOSIM also showed that overall the percentage species compositions did not differ significantly among months ($P > 0.05$; R statistic = -0.057). The points for fish trapping and trawling formed the tightest groupings, which is reflected in the low dispersion values, *i.e.* 0.254 and 0.464, respectively, whereas those for demersal gillnetting (large mesh), tuna gillnetting and pelagic (shark) longlining were the most widely dispersed, *i.e.* 0.808, 0.924 and 0.971, respectively. Those species that were shown to typify the catches obtained by each of the fishing methods are shown in Table 6.5.

6.3.6 *Size at maturity and size frequencies of the most abundant species*

The L_{50} s obtained for three shark species and one rhinobatid species that were abundant ranged from 707.9 mm in *Rhinobatus* sp. 1 to 2508 mm in *Alopias pelagicus*, which reached maximum total lengths of 840 and 3300 mm, respectively (Figs 6.6, 6.7;

Fisheries

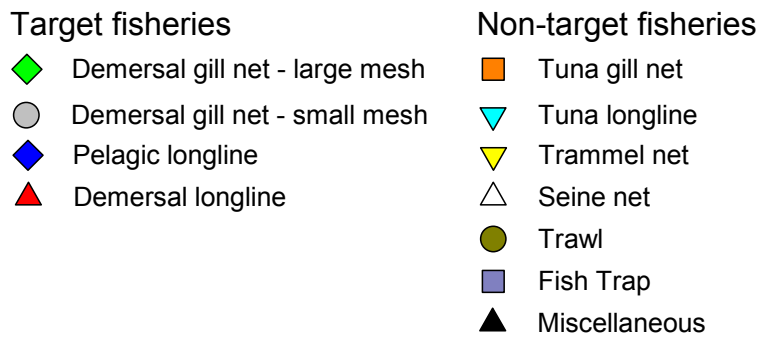
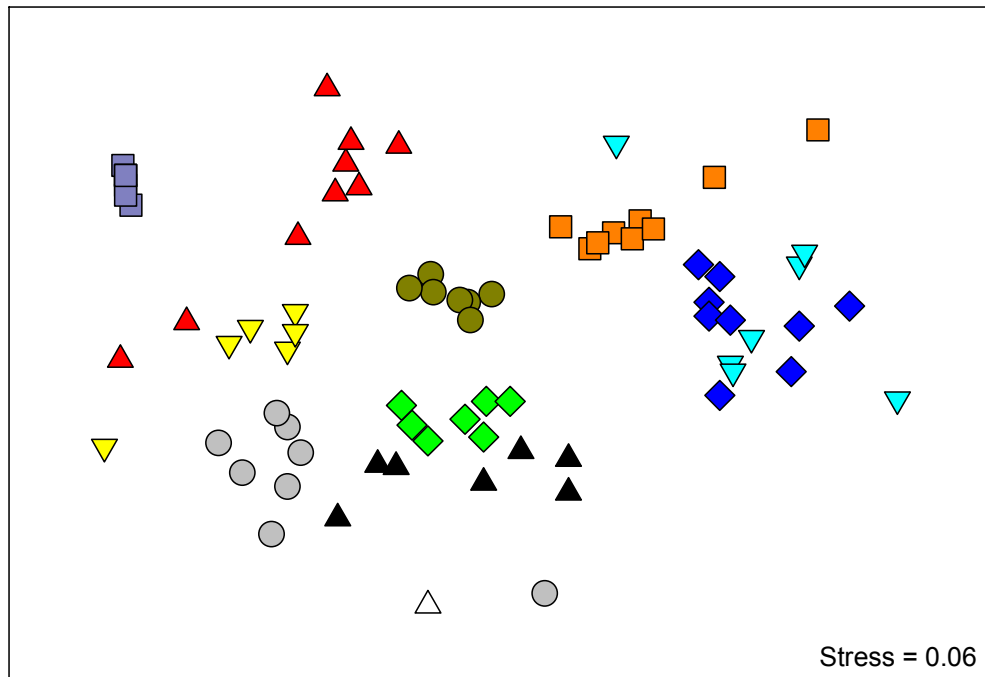


Figure 6.5 Non-metric multidimensional scaling ordination of the percentage contribution of each chondrichthyan in the samples for each of the target and non-target fisheries on each sampling occasion.

Table 6.5 Species typifying each of the main fishing methods in south-eastern Indonesia.

Fishing method	Species 1	Species 2	Species 3
Demersal gillnet (large)	<i>Himantura fai</i>	<i>Himantura</i> sp. sparse	
Demersal gillnet (small)	<i>Rhinobatus</i> sp. 1	<i>Aetoplatea zonura</i>	<i>Dasyatis kuhlii</i>
Pelagic (shark) longline	<i>Prionace glauca</i>	<i>Carcharhinus amblyrhynchos</i>	<i>Carcharhinus obscurus</i>
Demersal longline	<i>Squalus</i> sp. 3b	<i>Chiloscyllium punctatum</i>	
Tuna gillnet	<i>Carcharhinus falciformis</i>	<i>Sphyrna lewini</i>	<i>Mobula japonica</i>
Tuna longline	<i>Alopias pelagicus</i>	<i>Prionace glauca</i>	
Trammel net	<i>Himantura walga</i>	<i>Himantura</i> sp. sparse	<i>Himantura</i> sp. 1
Trawl	<i>Dasyatis zugei</i>	<i>Himantura walga</i>	
Fish trap	<i>Dasyatis kuhlii</i>		
Miscellaneous	<i>Himantura uarnak</i>	<i>Dasyatis kuhlii</i>	

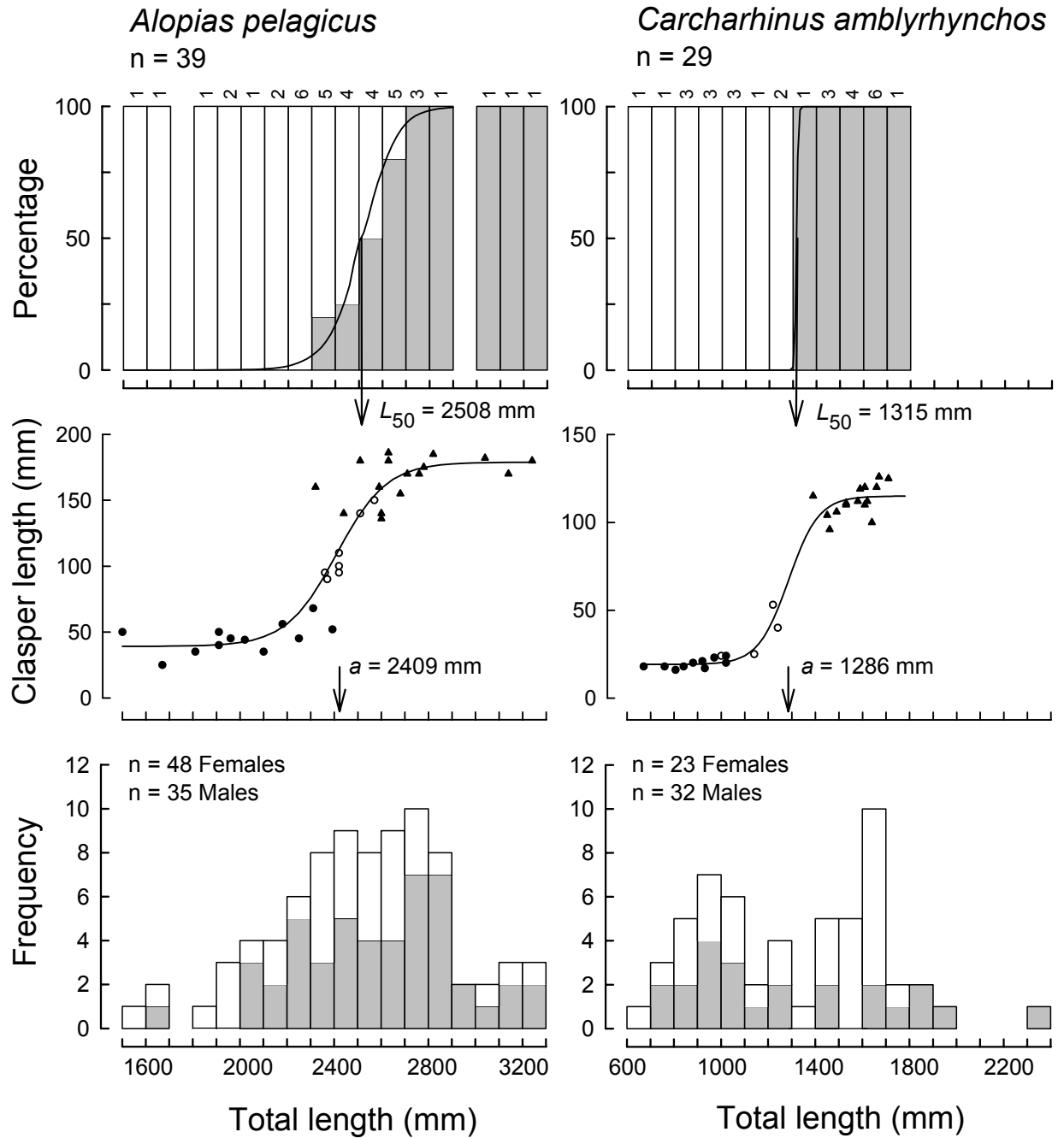


Figure 6.6 Size at maturity, clasper length vs size relationship and size frequency histograms of *Alopias pelagicus* and *Carcharhinus amblyrhynchos*. In this fig. and figs 6.7–6.9, the white bars in the maturity histograms (top) denote immature fish and the grey bars mature fish and arrows denote L_{50} or DW_{50} and a . In the clasper length vs size graphs in this fig. and figs 6.7–6.11, the closed circles refer to non-calcified claspers, open circles to incompletely calcified claspers and closed triangles to fully calcified claspers, and in the size composition graphs (bottom), grey bars denote females and white bars denote males.

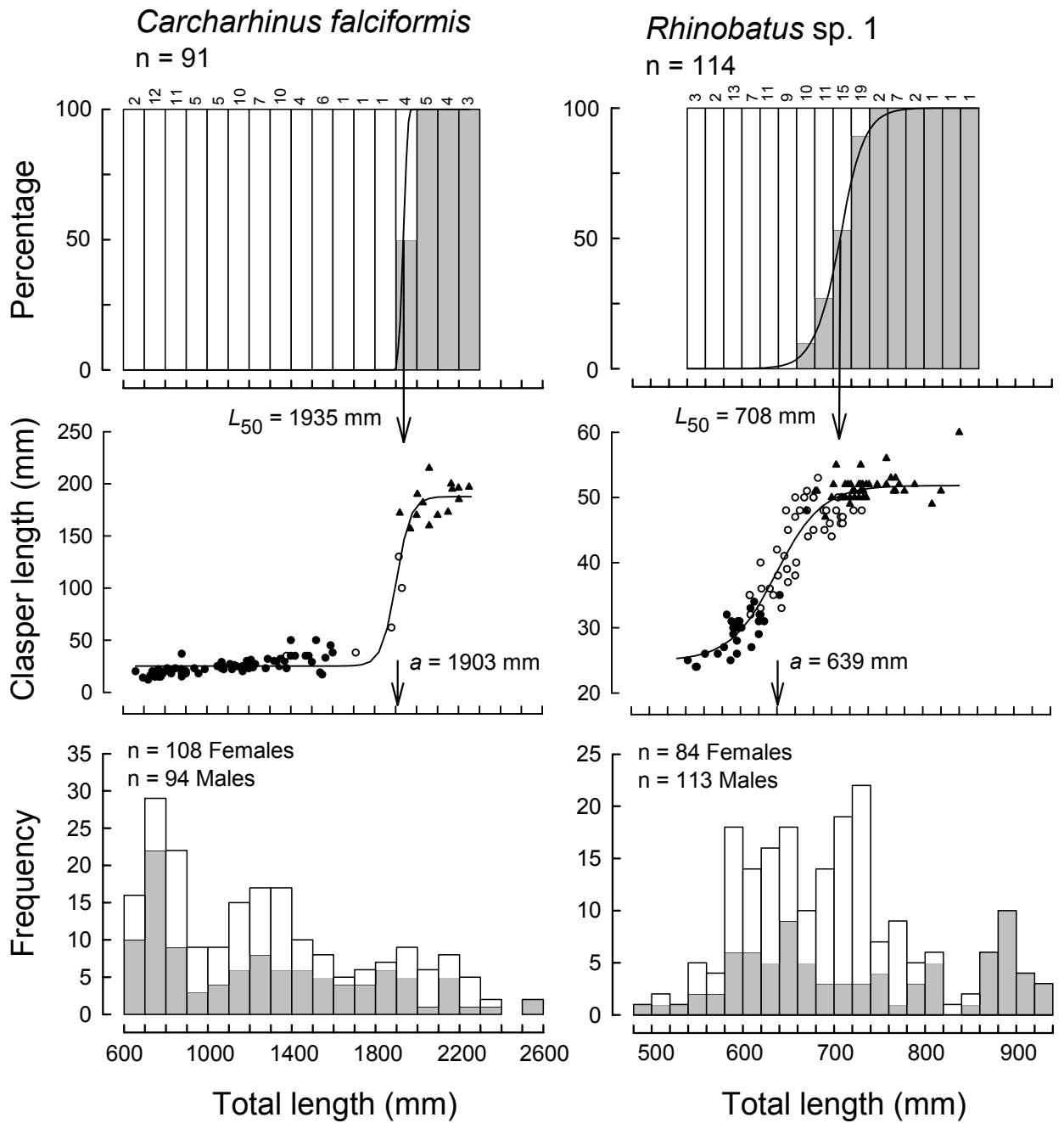


Figure 6.7 Size at maturity, clasper length vs size relationship and size frequency histograms of *Carcharhinus falciformis* and *Rhinobatus sp. 1*.

Table 6.6). The DW_{50} s obtained for the four abundant ray species ranged from 167 mm in *Himantura walga* to 476 mm in *Aetoplatea zonura*, which both reached maximum disc widths of 210 and 650 mm, respectively (Figs. 6.8, 6.9; Table 6.6). The modified logistic curve provided a good fit to the clasper length at body size for each of the eight species, except for *H. walga* for which there was an insufficient range of data (Figs 6.6–6.9). The trends exhibited by the curves emphasise that, in the case of each species, their claspers undergo a very marked relative increase in size over a narrow range in body size (Figs 6.6–6.9). This accounts for the size at inflection for this curve differing from the L_{50} or DW_{50} for each the seven species by only between 1.7 and 11.4% of the L_{50} or DW_{50} . A combination of the size-frequency distributions for males and the distribution of the males with mature claspers demonstrate that the catches of the males of *Carcharhinus albimarginatus*, *Carcharhinus brevipinna*, *Carcharhinus falciformis*, *Carcharhinus sorrah* and *Rhizoprionodon oligolinx* consisted predominantly of juveniles (Figs 6.7, 6.10, 6.11). In contrast, the catches of the males of *Prionace glauca* were represented almost entirely by mature individuals (Figs 6.10) and those of the males of *Alopias pelagicus* and *Carcharhinus amblyrhynchos* contained appreciable numbers of both juvenile and mature individuals (Figs 6.6).

The catches of the males of the ray species *Rhinobatus* sp. 1 and sp. 2, *Himantura* sp. sparse spot (*cf. gerrardi*) and *Aetoplatea zonura* comprised mainly juvenile fish (Figs 6.7, 6.9, 6.11), whereas those of *Mobula japonica* contained both juveniles and mature fish (Fig. 6.11). The catches of the males of three small dasyatid species, *i.e.* *Dasyatis kuhlii*, *Dasyatis zugei* and *Himantura walga*, were dominated by maturing and mature individuals (Figs 6.8, 6.9).

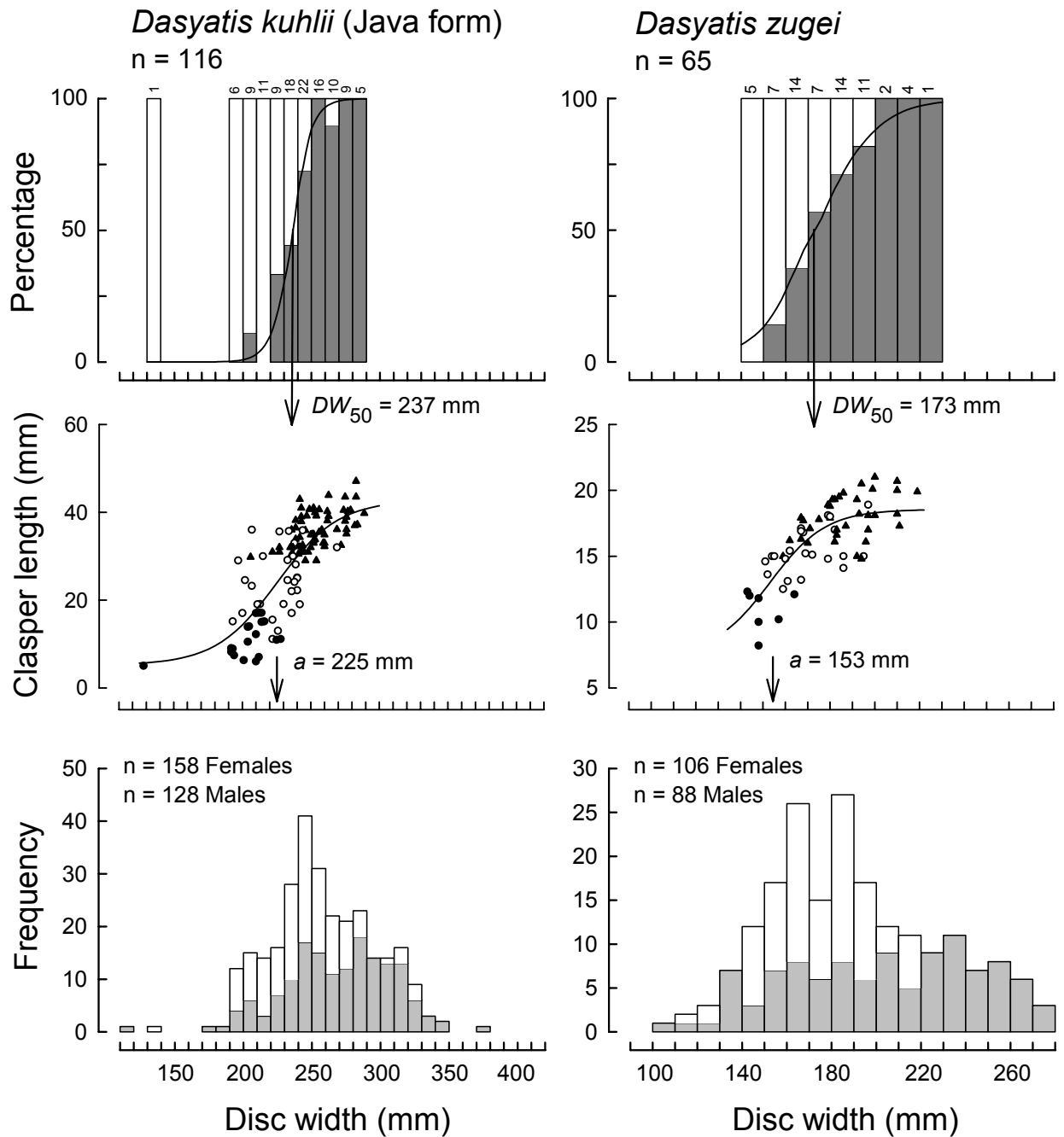


Figure 6.8 Size at maturity, clasper length vs size relationship and size frequency histograms of *Dasyatis kuhlii* (Java form) and *Dasyatis zugei*.

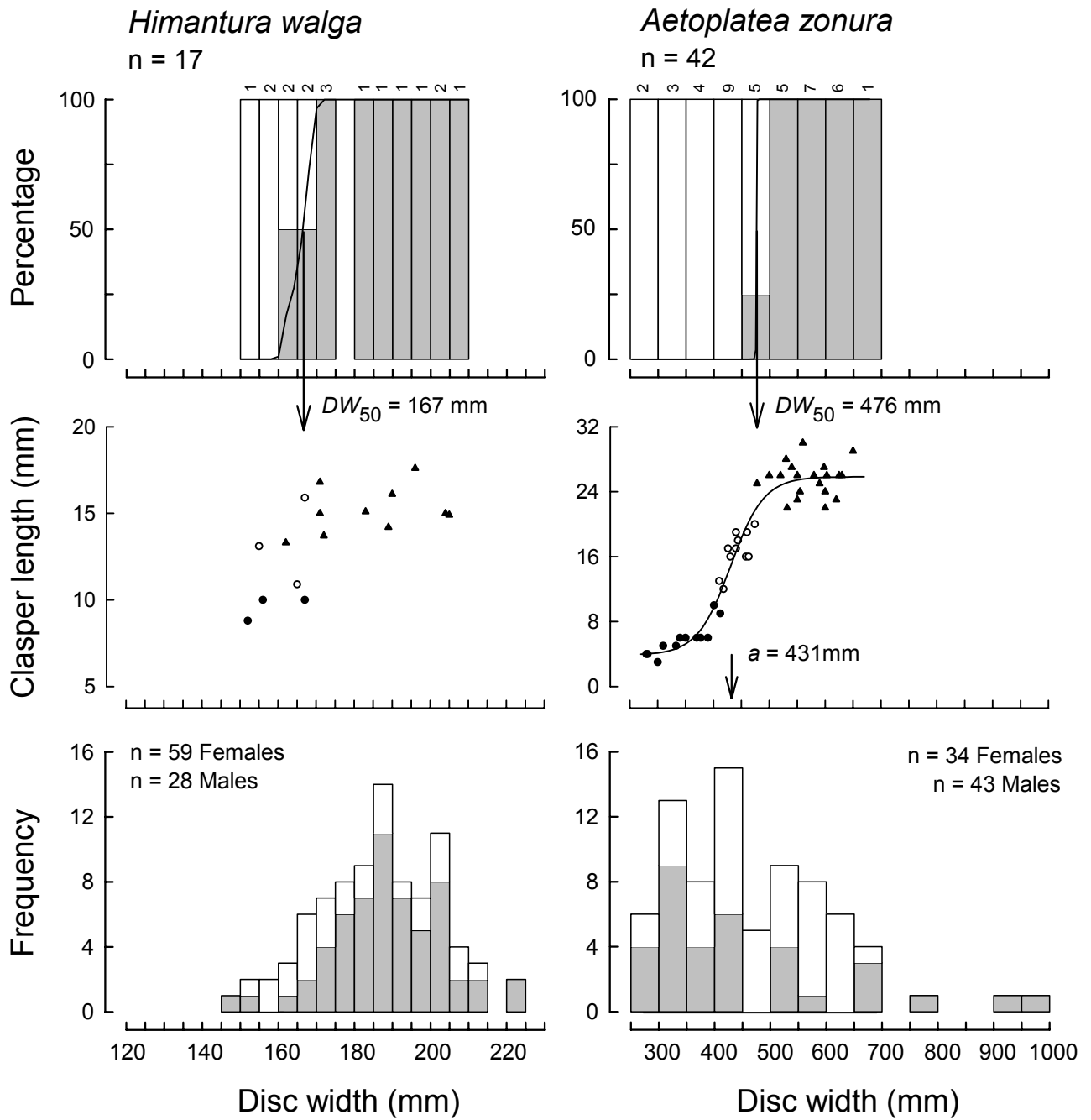


Figure 6.9 Size at maturity, clasper length vs size relationship and size frequency histograms of *Himantura walga* and *Aetoplatea zonura*.

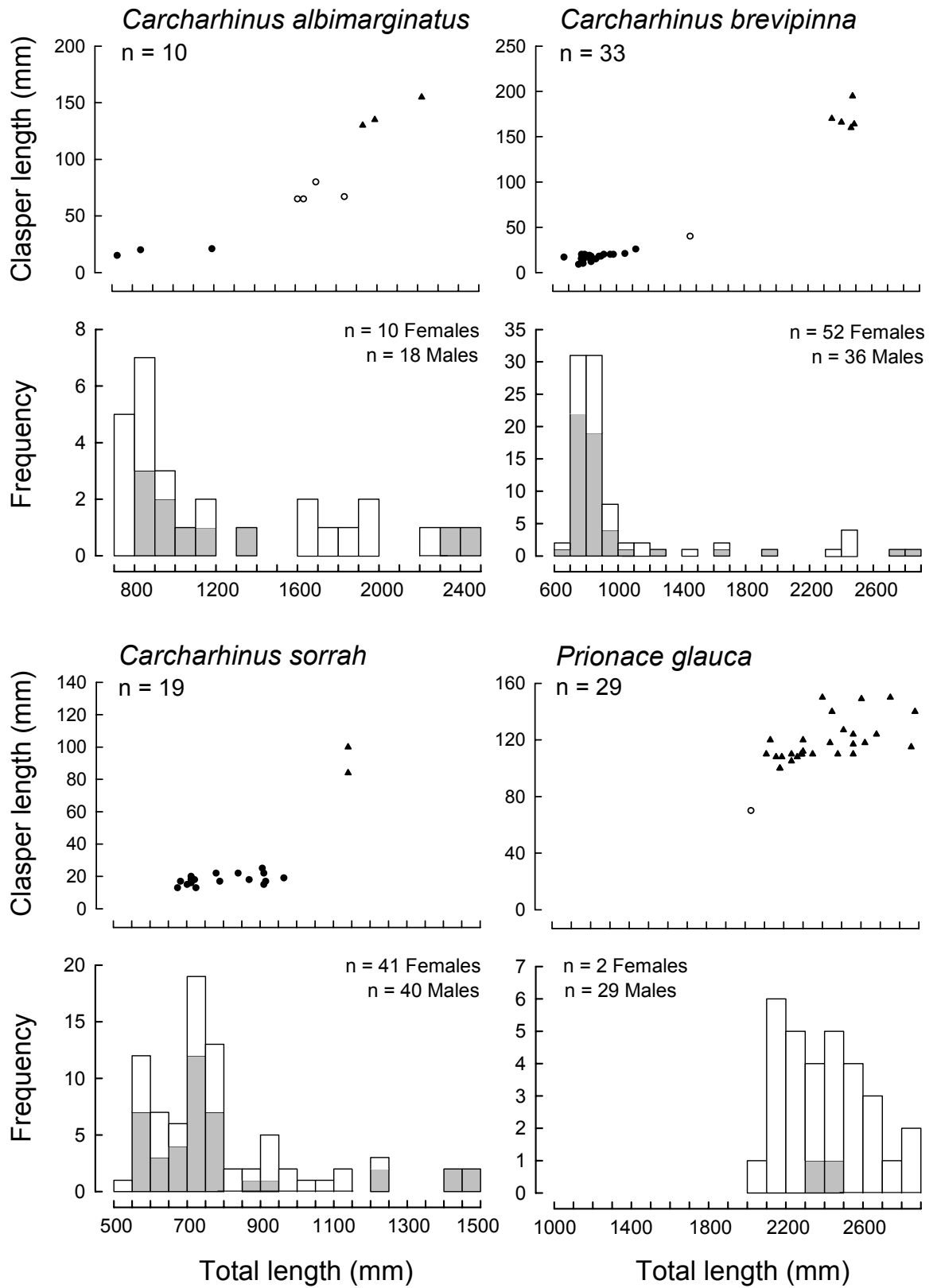


Figure 6.10 Clasper length vs size relationship and size frequency histograms of *Carcharhinus albimarginatus*, *Carcharhinus brevipinna*, *Carcharhinus sorrah* and *Prionace glauca*.

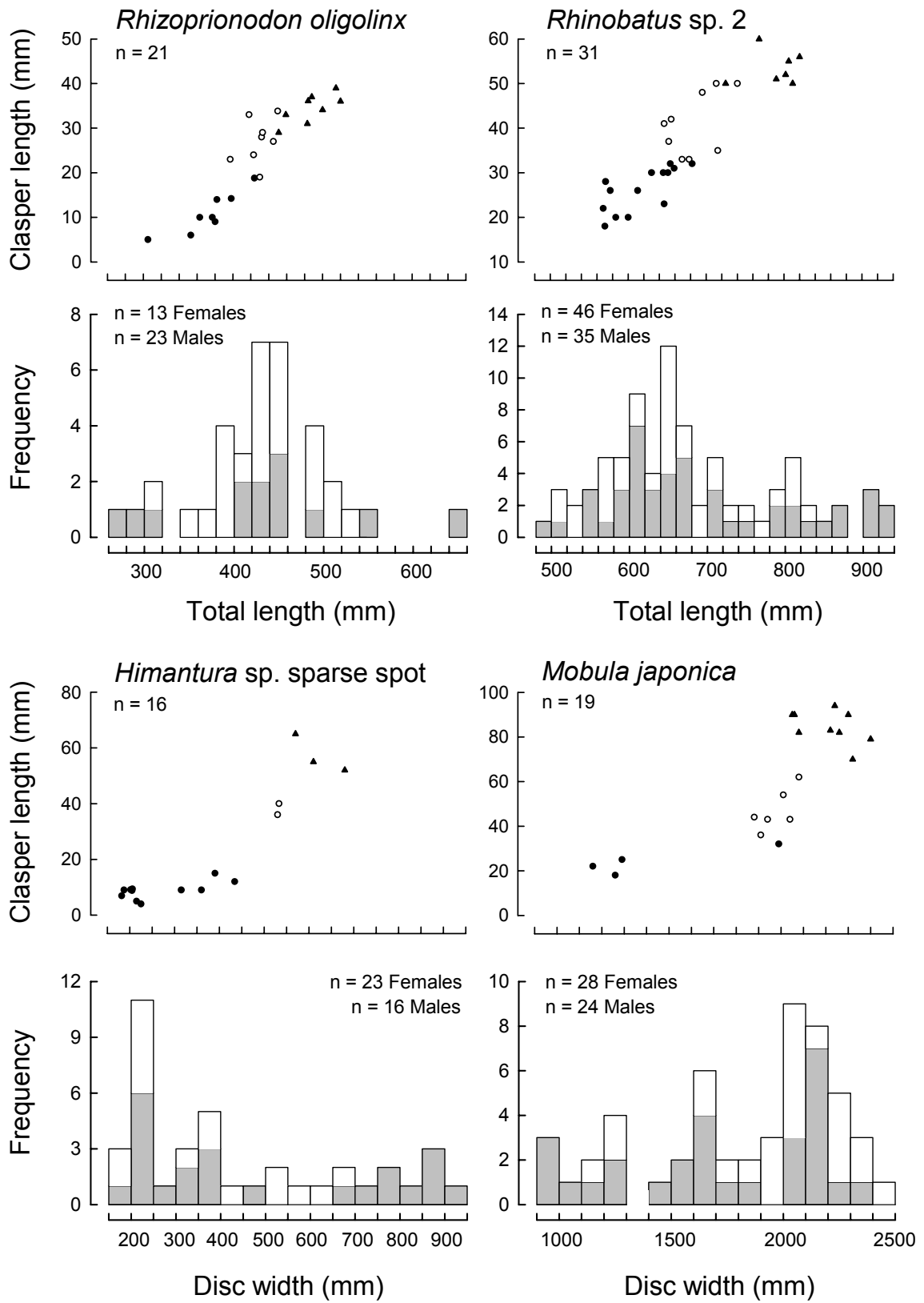


Figure 6.11 Clasper length vs size relationship and size frequency histograms of *Rhizoprionodon oligolinx*, *Rhinobatus sp. 1*, *Himantura sp. sparse spot* (*cf. gerrardi*) and *Mobula japonica*.

Table 6.6 The size at which 50% of males of the most abundant species attain maturity (L_{50} or DW_{50}) and the size at inflection (a) for the most abundant species. The lower and upper 95% confidence limits are given for each estimate. Note that a could not be calculated for *Himantura walga* due to the small number of small and immature fish.

Species	L_{50} or DW_{50} (mm)			a (mm)		
	Lower	Estimate	Upper	Lower	Estimate	Upper
<i>Alopias pelagicus</i>	2437.4	2508.3	2559.7	2348.1	2409.1	2470.0
<i>Carcharhinus amblyrhynchos</i>	1201.5	1315.0	1350.0	1251.5	1285.7	1319.9
<i>Carcharhinus falciformis</i>	1822.1	1935.0	1966.2	1891.4	1903.0	1914.5
<i>Rhinobatus sp. 1</i>	696.7	707.9	714.2	631.2	639.2	647.2
<i>Dasyatis kuhlii</i>	232.6	236.6	240.4	208.0	225.3	242.6
<i>Dasyatis zugei</i>	166.7	172.9	182.3	115.7	153.2	190.7
<i>Himantura walga</i>	159.9	166.6	169.0	-	-	-
<i>Aetoplatea zonura</i>	469.6	476.1	501.5	420.6	430.8	440.9

6.3.7 Taxonomic issues

Up to 49 of the chondrichthyan species recorded, *i.e.* 28 sharks, 20 rays and a single holocephalan could not be identified to the species level using taxonomic keys and have thus not apparently been described (see Table 6.2) and further taxonomic investigation is required to determine which of these are undescribed taxa. For example, the large number of potentially undescribed squalid species may be an overestimate and it is possible that those classified in a similar complex, *e.g.* *Squalus* sp. 2a, *Squalus* sp. 2b and *Squalus* sp. 2c, may represent only one species. Furthermore, all of the nine centrophorids observed were recorded as potentially undescribed species due to biological and/or morphological differences with the previously described members of this family (P. Last, pers. comm.). The single holocephalan observed was also recorded as an undescribed species as it is morphologically distinct from other previously described members of the *Hydrolagus* genus.

Another problem encountered was the presence of several forms of a single described species. For example, the commonly observed *Dasyatis kuhlii* from the landing site of Muara Angke (Jakarta) is quite distinct from the form observed at Kedonganan (Bali). The Java form is much darker and has a less distinct transverse band through the eyes and very few black flecks on the dorsal surface, whereas the Bali form is lighter with a very distinct transverse band through the eyes and a large number of black flecks on the dorsal surface (see Appendix I for colour images of both forms). Furthermore, the Bali form of *D. kuhlii* attains a considerably larger size, which is evident in the much larger size at first maturity in males than in the Java form. A further example can be seen with *Himantura gerrardi*, in which two other distinct forms were observed, *i.e.* a sparse spotted form and a yellow, no spot form, that could be readily distinguished from the true form at all stages of life (see Appendix I for colour images of all three forms). Since the separate forms, in both of the above cases, are quite distinct from the originally described form, they have each been classified as distinct species but further taxonomic investigation is required to validate this decision.

6.4 Discussion

6.4.1 Species compositions and unanticipated catches

It has been estimated that Indonesian waters contain more than 350 chondrichthyan species (P. Last, pers. comm.). The total of 139 species recorded during the present study was thus substantially less than the above value, reflecting, in part, the limited amount of deepwater fisheries (*i.e.* >200 m in depth) in this region. Those deeper waters contain a number of species, including certain centrophorids, etmopterids, somniosids, squalids, scyliorhinids and rajids, that were not recorded during the present study (P. Last, pers. comm.). The importance of deep waters in terms of chondrichthyan diversity is emphasised by the fact

that, although deepwater demersal longlining (60–600 m in depth) was probably the least extensive of the fisheries, the number of chondrichthyans caught by this fishery, *i.e.* 35, was the greatest of all of the chondrichthyan fisheries examined in Indonesia.

The large number of chondrichthyan species recorded at the landing sites in southeastern Indonesia during this study reflects the high diversity of this group of fishes in this region (Last & Stevens, 1994; Carpenter & Niem, 1998, 1999). In terms of number of species, numbers of individuals and total biomass, the catches were dominated by species belonging to the Carcharhinidae and Dasyatidae. This reflects that these two families are the most speciose and abundant elasmobranchs in the inshore waters of tropical and subtropical regions throughout the world (Compagno, 1984; Carpenter & Niem, 1998, 1999), where most of the elasmobranch fisheries are located.

The most abundant carcharhinids were *Carcharhinus falciformis*, *Carcharhinus sorrah*, *Rhizoprionodon oligolinx* and *Scoliodon laticaudus*, with the latter two species only being recorded at the landing site of Muara Baru. The last three species are small, *i.e.* <1500 mm in length, and commonly form large schools in inshore waters (Last & Stevens, 1994; Carpenter & Niem, 1998), which accounts for their particularly high abundance in the catches obtained by the inshore gillnet fishery. Although *Carcharhinus falciformis* is substantially larger than the other three species, this pelagic species is common in the relatively inshore tropical and warm temperate waters and thus occurs within the areas fished by the pelagic longline and gillnet fishers. There were also substantial landings of the sharks *Sphyrna lewini* and *Chiloscyllium punctatum*, which are also both common in the tropical Indo-West Pacific. Although relatively large numbers of the dogfish *Squalus* sp. 3b were recorded, the majority of squaloid sharks were only landed in low numbers, which reflects, in part, the limited amount of demersal fishing that was carried out in the deeper waters where squaloids typically occur.

The most abundant dasyatid species landed were *Dasyatis kuhlii*, *Dasyatis zugei*, *Himantura* sp. sparse spot (*cf. gerrardi*) and *Himantura walga*, which were landed in large numbers at Muara Angke. Each of these small stingrays is also abundant in commercial catches obtained by fishers in other south-east Asian countries (Carpenter & Niem, 1999). There were also substantial landings of several larger dasyatid species, namely *Himantura fai*, *Himantura jenkinsii*, *Himantura uarnacoides* and *Pastinachus sephen*, which are common in demersal inshore shelf regions of the tropical Indo-West Pacific. Other ray species that are abundant in the Indonesian region and which were landed in substantial numbers in Indonesia were *Rhynchobatus cf. australiae*, *Rhinobatus* sp. 1 and *Aetoplatea zonura*.

The recorded number of chondrichthyan species was greater at the landing sites of Kedonganan and Tanjung Luar, *i.e.* 79 and 72, respectively, than at Muara Angke and Cilacap, *i.e.* 52 and 44, respectively, even though the size of the fleet at the first two sites was far smaller. This apparent anomaly was due to a far larger number of fishing methods being employed at Kedonganan and Tanjung Luar and, as a consequence, a larger number of habitats were fished, *e.g.* oceanic, inshore and offshore pelagic, inshore and deepwater demersal waters.

Many of the populations of the small toothed sawfish *Pristis microdon* have declined markedly, and even apparently become extinct, in heavily-fished regions and consequently there are plans for facilitating the recovery of those populations (Carpenter & Niem, 1999). Only two individuals of this species were recorded during the present study of a very large number of elasmobranchs that were delivered to the various landing sites.

6.4.2 *Comparison of fishing methods*

The use of MDS ordination to analyse the species compositions of the chondrichthyan catches in Indonesian waters demonstrated that the compositions of the various species at each landing site on each sampling occasion reflected more the main fishing method employed by the fishers supplying those sites than the geographic distribution of the sites. For example, although the landing sites of Palabuhanratu and Cilacap are well separated geographically from Tanjung Luar (see Fig. 2.2), the points for the samples from all three sites lay in the same restricted region of the ordination plot. This reflects that pelagic longlining is the main method for catching chondrichthyans at each of these sites. In contrast, the points for the samples for each of the different fishing methods each formed relatively tight and discrete groupings and ANOSIM showed that they were significantly different ($P < 0.05$) in all pairwise cases (Fig. 6.5). Furthermore, the points for the samples for the three pelagic fisheries, *i.e.* pelagic (shark) longline, tuna longline and tuna gillnet, each formed groups in the right of the plot, whereas those for the inshore demersal fisheries, *i.e.* demersal gillnetting, trawling, trammel netting and fish trapping, lay in the left of the plot and those for the deepwater demersal longlining lay in the upper part of the plot (Fig. 6.5). It should be recognised, however, that the various fishing methods are used in different habitats. For example, seine netting is undertaken in nearshore, shallow waters, whereas demersal longlining is conducted over the substrate in deep water and tuna longlining is focused at the surface in oceanic waters.

A large number of species were also recorded in the demersal gillnet fishery for dasyatids (34) and the inshore gillnet fishery for tuna (31), whereas only one species was recorded from the fish-trapping fishery.

6.4.3 *The high level of exploitation on chondrichthyans in Indonesia*

The data collected in this study provide some indirect evidence that the abundance of some cartilaginous species in Indonesia may have undergone a marked decline as a result of the very high level of exploitation. Such a view is supported, in particular, by comparisons between the species compositions in the catches obtained by the demersal tangle–gillnet fishery operating out of the landing sites of Muara Angke, Bena Harbour and Merauke. Although the boats operating at each of these sites fish in different regions, they use similar gear, fish in similar habitats for a similar period of time and land approximately the same quantity of elasmobranchs per trip (see Table 6.4). However, a typical catch obtained by the fishery at Muara Angke, which operates in the heavily-fished areas of the Java Sea and West Sumatra, would include less than 2% rhynchobatids, whereas the fishery at Bena Harbour and Merauke, which operates in the moderately fished areas of the Banda and Arafura Seas, would catch 30–50% of these rays. The particularly heavy fishing pressure on rhynchobatids in the Java Sea and West Sumatra reflects that this group is one of the most sought after elasmobranchs in south-east Asia (particularly Indonesia), where the dorsal fins and upper caudal fin fetch very high prices. For example, a set of fins from a single individual has been reported to fetch up to about Rp 900 000 or US\$396 kg⁻¹ (Chen, 1996). Furthermore, the skins and flesh of these rays are also of good quality and thus fetch a reasonable price. A further indication of an apparently deleterious effect of fishing on rhynchobatids is provided by changes in the gillnet fishery that was established for these rays in the Aru Islands in the mid 1970s. This fishery expanded rapidly to reach a peak in 1987, when more than 500 boats were involved, but, as a result of declining catches, the number of boats subsequently fell to only 100 in this area in 1996 (Chen, 1996).

A similar high and unregulated level of exploitation on chondrichthyans has been recorded in the Mexican artisanal shark fishery in the Gulf of Mexico (Castillo-Géniz *et al.*,

1998). As in Indonesia, these artisanal fisheries provide an important source of food and employment in Mexico. However, the Mexican shark fishery is based predominantly on the seasonal abundance of a number of carcharhinid and sphyrnid species that make annual migrations southwards from USA territorial waters (Castillo-Géniz *et al.*, 1998), whereas the Indonesian artisanal fisheries are much more diverse and catch large numbers of chondrichthyans throughout the year. Thus, any form of future regulation in Indonesia may need to concentrate initially on individual fisheries rather than the chondrichthyan fisheries as a whole.

The greatest concern for the chondrichthyan fisheries in Indonesia is the high level of unreported catches and the lack of any real management plans. Dudley & Harris (1987) found considerable deficiencies in the methods for collecting data on fisheries landings and estimated that the landings recorded can be inaccurate by factors of between 0.8 and 3.8 times. An example of attaining inaccurate data on landings was observed at the site of Muara Angke, where the fisheries officers (*Dinas Perikanan*) reported figures of 8–10 tonnes landed per demersal gillnetting boat, whereas the Harbour Master, who requires accurate boat tonnage data for port authorities, reported landings of closer to 30 tonnes. This type of underestimation by the *Dinas Perikanan* has been observed for a number of fisheries in Indonesia (B. Fagan, pers. comm.) and highlights the need to establish procedures whereby accurate data on landings can be recorded. The acquisition of such accurate data are essential for facilitating the development of appropriate management plans for conserving the chondrichthyan fisheries resources of Indonesia. Since concerns over a lack of management in this country have become widespread in both Indonesian and Australian scientific and fisheries organisations, it is hoped that a National Plan of Action (NPOA) for chondrichthyans will be developed in the near future (S.J.M. Blaber, pers. comm.).

6.4.4 *Size compositions*

The high proportion of juveniles in the catches of the males of seven of the carcharhinid species demonstrates that the individuals of certain shark species are being exploited in their nursery areas and are thus prevented from reaching maturity. Furthermore, since female elasmobranchs typically attain maturity at either similar or larger sizes than their males, it is assumed that the females of the above species are also caught prior to reaching maturity and thus before they produce young. A large number of juveniles of carcharhinid and sphyrnid sharks have also been recorded in landings of the inshore artisanal shark fishery in Mexico, in which they represented more than 90% of the total recorded landings (Castillo-Géniz *et al.*, 1998). From studies carried out elsewhere in the world, carcharhinid and sphyrnid sharks have been shown to use certain habitats in inshore waters as nursery areas for variable periods (Springer, 1967; Blaber *et al.*, 1985, 1989; Simpfendorfer & Milward, 1993).

The proportion of mature individuals in the catches of species such as *Dasyatis kuhlii* (Java form), *Dasyatis zugei* and *Himantura walga* were high, which is probably attributable to gear selectivity. These species, which are caught by trawling, and also by trapping in the case of the first species, are born at a very small size, *i.e.* with disc widths of only 70 to 150 mm (see Appendix II), and thus recently-born individuals would be likely to pass readily through the mesh used in both the trawl nets and fish traps. The catches of other species, such as *Prionace glauca*, were represented almost entirely by mature fish, indicating that the fishing gear does not capture their juveniles or that the juveniles of these species occur in habitats where fishing pressure was limited. Juveniles of *P. glauca* are known to occur in separate areas from the adults in other regions (J.D. Stevens, pers. comm.).

6.4.5 Undescribed species and the importance of taxonomic resolution

Although there are some published data on the total annual chondrichthyan landings at various regions in Indonesia (see *e.g.* Dudley & Harris, 1987; Bonfil 1994; Chen 1996), there are very limited published data on the species and size compositions of these landings. The large number of apparently undescribed species recorded during this study, *i.e.* up to 49, highlights the limitations of the taxonomic data available for chondrichthyans in Indonesia. Indeed, Dudley & Harris (1987) stated that the one of the greatest problems with the methods used for recording chondrichthyan landings in Indonesia was the lack of taxonomic detail. Risk assessment analysis has previously been used to determine which elasmobranch species within a fishery are under the greatest threat and are therefore less sustainable (Stobutzki *et al.*, 2002). Without accurate species composition data, such risk analysis cannot be performed and the level of threat and degree of sustainability of each chondrichthyan species cannot be determined.

Since this study represents the first detailed account of the chondrichthyan fauna of Indonesia, and as Indonesia is reported to have one of the highest rates of generic endemism in the world (Anon., 1995), the collection of a relatively large number of undescribed and often endemic species was anticipated (P. Last, pers. comm.). Indeed, the majority of the undescribed species appear to be endemic to Indonesia. A number of species, *e.g.* *Pastinachus* sp. 1 and *Chiloscyllium* sp. 2, have previously been recorded in surveys of fishery landing sites in Borneo (P. Last, pers. comm.).

In summary, this study provides the first detailed data on species and size compositions of chondrichthyans in the target and non-target fisheries in Indonesia. The large number of species recorded reflects the high diversity of fishes found in the tropical waters of south-east Asia. A variety of target and non-target chondrichthyan fisheries were observed during the study, ranging from seine netting over intertidal sand flats to demersal

longlining in 600 m of water. The majority of habitats within these waters are under a high level of fishing pressure with only the deepest regions, *i.e.* >600 m in depth, not being heavily fished. These target and non-target chondrichthyan fisheries in south-eastern Indonesia are unregulated and the formation of management plans to assist the conservation of chondrichthyan stocks in these waters is required.

Chapter 7

General discussion

7.1 Resource partitioning by elasmobranchs in Shark Bay

The studies described in Chapters 3 and 4 represent one of the first attempts to use appropriate statistical analyses, such as MDS ordination, to explore whether the main elasmobranch species found in a particular environment partition the resources of that environment on spatial, temporal and trophic scales. Ross (1986) concluded that the partitioning of resources among co-occurring abundant fish species reduces the potential for interspecific competition and that food and then habitat are the resources most likely to be subjected to such partitioning.

My study demonstrated that the food resources within the nearshore shallows of Herald Bight are partitioned within and amongst the four elasmobranch species that are most abundant in these waters, *i.e.* the ray *Rhinobatus typus* and the sharks *Carcharhinus cautus*, *Rhizoprionodon acutus* and *Negaprion acutidens*. Thus, the ray *R. typus* fed almost exclusively on penaeid prawns and portunid crabs, whereas the three shark species ingested predominantly teleost species but in varying amounts. Furthermore, the diets of each species changed with increasing body size, which would have reduced the likelihood of intraspecific competition for food. The dietary composition of *R. typus* was also shown to differ seasonally, and particularly between winter and both summer and spring, presumably reflecting seasonal changes in the relative abundances of the different prey of that species.

The different habitats in the nearshore shallows of Herald Bight were shown to be partitioned amongst the main elasmobranch species present in those waters. For example, *Carcharhinus cautus* and *Negaprion acutidens* were caught almost exclusively in unvegetated sites, particularly near dense mangroves, whereas *Rhizoprionodon acutus*, *Carcharhinus brevipinna* and *Chiloscyllium punctatum* were collected predominantly or exclusively from over seagrass. Furthermore, within the three unvegetated habitats sampled, the number of elasmobranch species and number of individuals of elasmobranchs

were greater at the site near dense mangroves than at the one where no vegetation was present nearby. These two biotic variables were also greater in the summer and autumn than in the winter and spring, when water temperatures were lower.

7.2 Growth of *Carcharhinus cautus* during pre- and postnatal life

The data presented in Chapter 5 showed that a smooth, monotonically increasing growth curve could be used to describe the way in which the lengths of *Carcharhinus cautus* increased with age throughout the whole of the life of this shark, *i.e.* from the onset of embryonic growth. Such growth curves were also derived previously using the disc widths at age of three species of urolophids, *i.e.* *Urolophus lobatus*, *Trygonoptera personata* and *Trygonoptera mucosa*, which belong to a morphologically very different group of elasmobranchs (White *et al.*, 2001; 2002).

I have explored quantitatively under what circumstances it would be appropriate to switch from using the conventional, three-parameter von Bertalanffy growth curve to a more complex growth curve, *e.g.* the four-parameter Schnute or five-parameter Schnute and Richards growth curve. The Schnute growth curve produced, in three of the four cases examined, a statistically significant improvement of the fit to the length-at-age data than that which was achieved by employing the von Bertalanffy curve. Since the presence of a large number of values for the lengths at age of the females and males of *C. cautus* resulted in the likelihood ratio test being highly sensitive, the biological significance of such improvement to the fit was also investigated. It was considered that, if the maximum percentage difference between the lengths derived from the two curves at any age, except those of the youngest fish, exceeded 5%, the difference was biologically significant and thus the Schnute curve should be employed to describe the lengths at age in such cases. Although it is preferable to use the von Bertalanffy growth curve whenever possible, as it is

simpler and allows comparisons to be made with other species, the use of a more complex growth curve for a particular species is justified if it provides both a statistically significant improvement to the fit of the sizes at age and an improvement that is considered biologically significant.

7.3 Exploitation of chondrichthyans in Indonesia and future research needs

The work in south-eastern Indonesia demonstrated that a large number of chondrichthyan species (139) are exploited by the target and non-target fisheries operating in this region. Since there were no quantitative data on the species composition of fisheries in south-eastern Indonesia, the focus of this work was initially placed on obtaining details of the species and their size compositions for each of the fishing methods used to supply fish at a number of selected landing sites. The results emphasise that the compositions of the catches at a landing site were influenced to a very large degree by the types of fishing gear used by the fishers supplying those landing sites and the types of environment in which the fish were caught. Analysis of the size at maturity of the males of the most abundant elasmobranch species showed that considerable numbers of many of these species were being caught before they reached maturity, which does not auger well for the conservation of these resources.

In view of the possible detrimental impacts of fishing on certain elasmobranch species in Indonesia, it is important that work should be undertaken to determine the extent to which those species are part of stocks shared with Australia. Such information could then be used to develop a common policy for conserving those stocks in the two regions. The development of appropriate management strategies for conserving those elasmobranchs requires the acquisition of more biological data on those species that dominate the catches, *e.g. Alopias pelagicus*, *Carcharhinus falciformis* and *Rhynchobatus cf. australiae*.

Fisheries managers in Indonesia are faced not only with the problem of a paucity of quantitative data on the species composition of chondrichthyan catches at the various landing sites, but also a high level of unreported catches. For example, although most fishers in Indonesia land whole sharks, those operating the large commercial tuna longline boats retain only their fins, which are exported to the oriental “shark-fin” market. The catches of the latter sharks are thus not reported. Thus, although Indonesia has the highest reported annual elasmobranch landings in the world, the recorded catches represent a gross underestimate of the actual number of elasmobranchs caught. Consequently, there is a need for a dramatic improvement in the ways that data on the catches landed at the different landing sites are collected.

It is anticipated that the field guide presented in Appendix I will be published as an identification guide, with bilingual species accounts and colour photographs, and that this will be circulated throughout Indonesia. This will enable local chondrichthyan species to be identified and thus allow more detailed species composition data to be collected from landing sites in the future.

7.4 Batoids: the forgotten elasmobranchs

Although there is a relatively large amount of published data on the reproductive biology and age and growth of sharks (particularly carcharhinids), there have been few published studies on these aspects of the biology of batoids. The importance of acquiring such data for the dasyatid batoids, in particular, is emphasised by this family alone containing more than 60 species and being the dominant batoid family in the tropical and sub-tropical regions of the world. However, there have been only a few studies on the reproductive biology of species of *Dasyatis*, a genus that contributes *ca* 50% of the total number of species in this family. The preliminary reproductive studies carried out on *Dasyatis kuhlii*,

Dasyatis zugei and *Himantura walga* during this thesis (see Appendix II) represent the first such studies on any dasyatid species in south-eastern Indonesia. There has apparently been only one study on the age composition and growth of any dasyatid species and, even in this case, the results are rather inconclusive (Ismen, 2003). Despite the paucity of data on the biology of batoids, this group of cartilaginous fishes is highly exploited by both target and non-target fisheries throughout the world, *e.g.* south-east Asia. In the future, elasmobranch research should focus, to a greater extent than in the past, on obtaining the types of biological data for those species of batoid that are heavily exploited and which are required for managing these species.

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Appendix II

Biology of three abundant dasytid rays (Batoidea: Dasyatidae) from the Java Sea in south-eastern Indonesia

Introduction

Fisheries for batoids are particularly important in south-east Asia, and especially in Indonesia (Chen, 1996; Carpenter & Niem, 1999). The reported elasmobranch landings in Indonesia consist of *ca* 66% sharks and *ca* 34% rays, of which, members of the Dasyatidae are, by far, the most dominant species (Carpenter & Niem, 1999; Stevens *et al.*, 2000). The Dasyatidae (stingrays) contain more than 60 living species, each belonging to one of five poorly-defined genera that require taxonomic resolution (Carpenter & Niem, 1999). The taxonomic problems posed by this family are highlighted by the results of the present study, in which approximately 11 of the 29 dasyatid species recorded in south-eastern Indonesia between April 2001 and February 2003 were undescribed species (see Chapter 6).

Although there is a dearth of published information on the biology of most dasyatid species throughout the world, there are sound data on the reproductive biology of *Dasyatis centroura*, *D. sabina* and *D. sayi* (see Hess, 1959; Struhsaker, 1969; Snelson *et al.*, 1988, 1989; Capapé, 1993; Johnson & Snelson, 1996). There are also limited biological data for *D. guttata*, *D. longa* and *D. pastinaca* (see Thorson, 1983; Garayzar *et al.*, 1994; Ismen, 2003). However, none of the above six species are found in south-east Asia and thus there is no biological information on any of the dasyatid species found in this region.

Furthermore, although *Himantura* is the second largest genus in the Dasyatidae, there are no published data on the biology of any of the species that belong to this genus. The poor taxonomic data and lack of sound biological data for dasyatids in south-east Asia, and indeed for the whole of the Indo-West Pacific, restricts the ability of managers to develop plans for conserving these species, which are becoming increasingly exploited.

The aim of this component of the thesis was to determine the size compositions and aspects of the reproductive biology, *i.e.* timing of ovulation and parturition, size at maturity and fecundity, of three of the most abundant dasyatids, *i.e.* *Dasyatis kuhlii*, *Dasyatis zugei*

and *Himantura walga*, recorded at fish landing sites in south-eastern Indonesia. Preliminary studies of the age compositions and growth of the most abundant of these three species, *i.e.* *D. kuhlii*, were also undertaken. Finally, the reproductive data for the above three species are compared with those published for the other five members of the genus *Dasyatis* for which there are such data.

Methods

Sampling location and regime

Samples of *Dasyatis kuhlii*, *Dasyatis zugei* and *Himantura walga* were purchased on seven occasions between June 2001 and February 2003 from the landing site of Muara Angke, which is located on the mouth of the Angke River in the province of Jakarta (Fig. 2.2 in Chapter 2). Every attempt was made to obtain samples of 30 to 50 individuals of each of these three species of rays on each of these occasions, the cost of which ranged from Rp5000 to 7500 or *ca* AUD1.00 to 1.50 per kilogram. The rays were collected before they reached the public markets and were immediately stored on ice, after which they were transported to the local fisheries laboratory for processing.

Reproductive biology

The disc width (to nearest 1 mm), total mass (to nearest 1 g), maturity stage and sex of each ray were recorded. In the case of males, the length of the left clasper, from its insertion in the pelvic fin to its tip, was recorded to the nearest 1 mm and the extent of calcification of both claspers, *i.e.* non-calcified, not fully calcified or fully calcified, was noted. The maximum diameter of the largest oocyte (MOD) in the functional ovary of each mature female was measured to the nearest 0.1 mm and, in the case of pregnant females, a record kept of the disc width (to nearest 1 mm) and sex of all embryos.

Using the criteria shown in Table 1 in White *et al.* (2001), each individual female or male ray was assigned one of the following maturity stages. For females, the maturity stages were (1) immature, (2) maturing virgin, (3) mature, non-pregnant, (4) mature, pregnant and (5) mature, post-partum, whereas for males they were (1) immature, (2) maturing virgin, (3) mature, non-reproductive and (4) mature, sexually active. By definition, the females and males at maturity stages 1 and 2 would not have been capable of reproduction and are thus collectively referred to as immature, whereas the females and males at maturity stages 3–5 and 3–4, respectively, would have been either capable of or in the process of reproducing and are thus collectively referred to as mature.

The disc widths at which 50% of both females and males of each species attain maturity (*i.e.* the DW_{50} at first maturity) were derived by fitting the logistic regression,

$$p_{DW} = \frac{1}{1 + \exp\left[-\ln(19) \frac{(DW - DW_{50})}{(DW_{95} - DW_{50})}\right]},$$

to the proportion of those rays that were mature at disc width DW , where DW_{50} and DW_{95} are constants and \ln is the natural logarithm. Maximum likelihood estimates of the parameters were obtained using the routine SOLVER in Microsoft™ Excel, by calculating the likelihood of immature and mature individuals as $1 - p_{DW}$ and p_{DW} , respectively. The reported estimates of the parameters were determined as the median values derived from 200 sets of randomly resampled data, with the same sample size drawn from the data on observed maturity status at disc width for female and male rays, respectively.

Age and growth

In the case of all individuals of *Dasyatis kuhlii*, a section of 5–10 vertebrae was excised from the posterior region of that part of the vertebral column that becomes exposed when

the viscera are removed. The excised section of the vertebral column was then stored frozen. The ways in which the vertebrae were treated for ageing purposes and the marginal increments were measured are described in Chapter 5. However, in this case, counts of growth zones and measurements of marginal increments (to the nearest 0.1 μm) were both recorded using the imaging software Leica IM1000, which acquired the image via a Leica DC300 digital camera attached to a Leica MZ7.5 dissecting microscope.

Since neither the conception nor parturition of *D. kuhlii* occurred at a particular time of the year (see later), it was not possible to use a mean conception and parturition date for the individuals of this species for determining their growth curves from the times of conception and birth. von Bertalanffy and Schnute growth curves were thus fitted to the individual disc widths of each female and male of *D. kuhlii* vs the number of translucent zones. The data were fitted by minimizing the sum of squared deviations between the observed and predicted disc widths using a nonlinear regression in SPSS (SPSS Inc., 1999) and the routine SOLVER in Microsoft™ Excel. Details of the von Bertalanffy and Schnute growth equations, and the likelihood ratio test used to determine whether there were significant differences between the two different growth curves and between the curves derived for each sex, are given in Chapter 5. It should be noted that, in the case of *D. kuhlii*, the disc width rather than total length was measured and thus, in the growth curve parameters, L is replaced by DW .

Results

Monthly trends in maximum oocyte diameter and embryo disc widths

The mean monthly MODs for mature females of *Dasyatis kuhlii* in the months between January and August ranged from 5.5 to 11.2 mm and did not show any consistent pattern of change (Fig. 1). Furthermore, oocytes with a wide range of maximum diameters were

present in each month sampled and very large ova, *i.e.* >15 mm, were found in all months except August (Fig. 1). Similarly, the mean monthly MODs for mature females of *Dasyatis zugei* and *Himantura walga* typically ranged widely in most months (Fig. 1). Since the monthly MODs of all three species did not follow a distinct trend during the year, ovulation does not occur during a restricted period of the year.

The mean monthly embryo disc widths of *D. kuhlii* increased from 29.5 mm in January to 87.0 mm in March and remained at between 69.3 and 107.3 mm in the subsequent months sampled (Fig. 2). However, the embryo disc widths varied greatly in most months and fertilised eggs and/or very small embryos were observed in February, March and May. Thus, conception was occurring over at least four months, *i.e.* from February to May, and possibly throughout the whole year. Since the disc width of the smallest free-swimming *D. kuhlii* was 118 mm and that of the largest embryo was 145 mm, the disc width of this species at birth would be approximately 120–145 mm. Furthermore, as embryos with disc widths approaching that of recently-born individuals, *i.e.* *ca* 120 mm, were recorded in all months sampled except January and July (Fig. 2), parturition was taking place over a long period.

The mean monthly embryo disc widths of *D. zugei* ranged from 10.8 mm in May to 61.5 mm in March (Fig. 2). Fertilised eggs were observed in the functional uterus of three female *D. zugei* in May. Since only ten embryos or fertilized eggs were observed in this species in the limited number of months sampled, it was not possible to determine the approximate time of conception or parturition. The disc width of the smallest free-swimming *D. zugei* was 104 mm and that of the largest embryo was 71 mm. Thus, the disc width at birth of this species presumably lies between 70 and 100 mm. The mean monthly embryo disc widths of *H. walga* in March and May were 25.7 and 58.8 mm, respectively (Fig. 2). Fertilised eggs were observed between March and August, indicating that

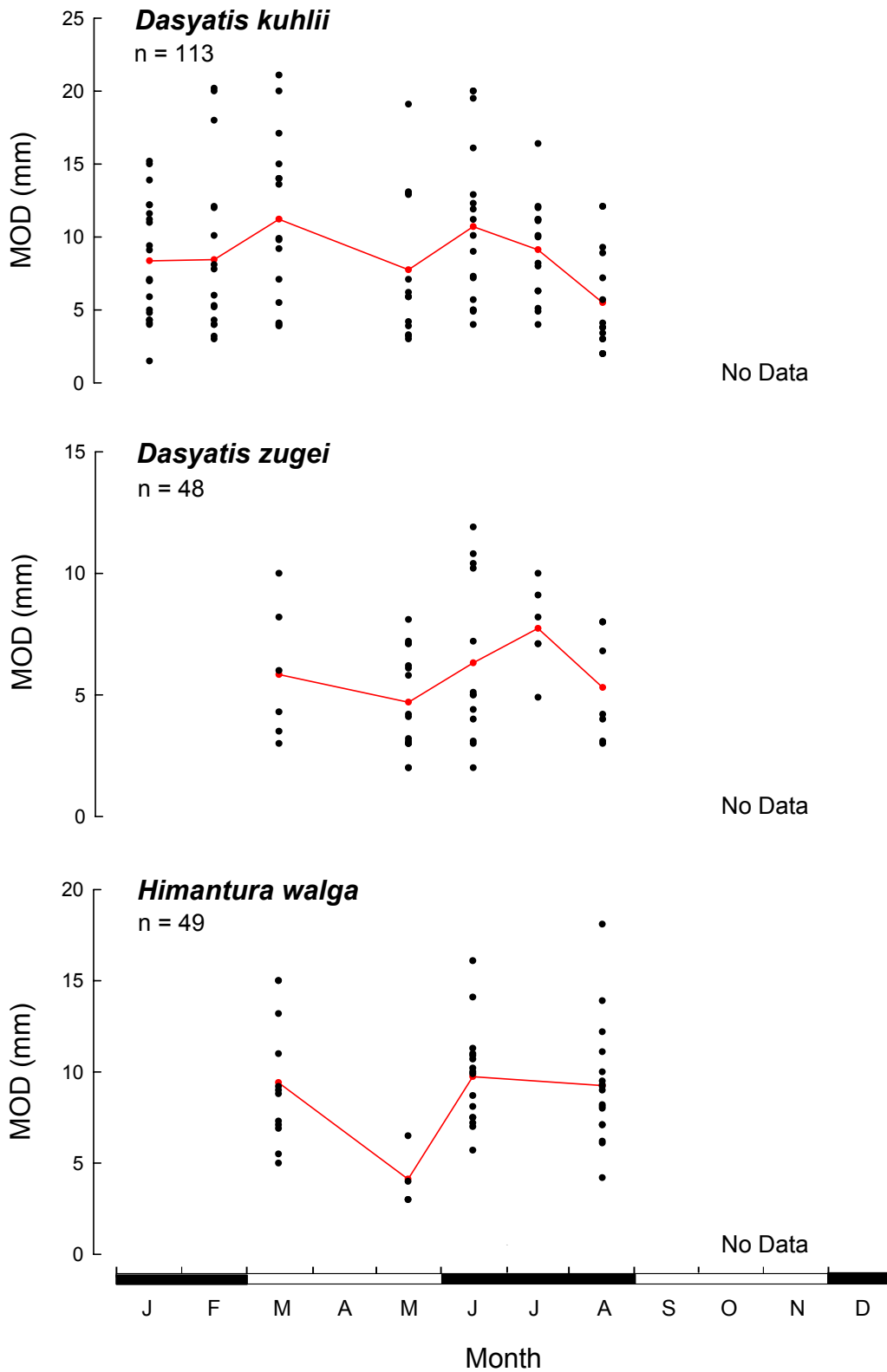


Figure 1 Monthly maximum oocyte diameters (MOD), including their means, in the functional (left) ovary of mature females of *Dasyatis kuhlii*, *Dasyatis zugei* and *Himantura walga*.

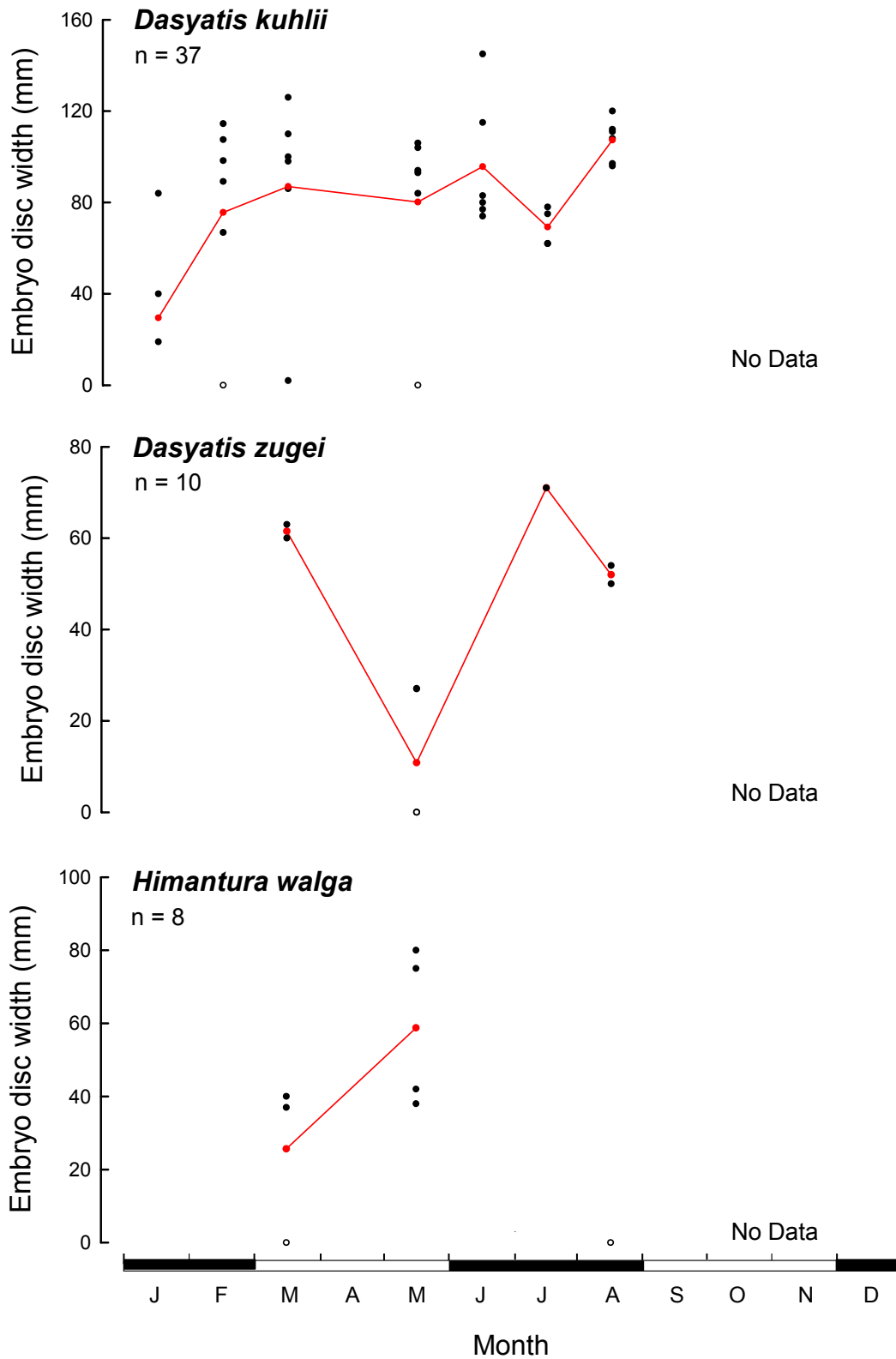


Figure 2 Monthly embryo disc widths, including their means, of *Dasyatis kuhlii*, *Dasyatis zugei* and *Himantura walga*. Solid circles denote embryos and hollow circles fertilised *in utero* eggs with unmeasurable embryos.

conception was occurring in at least these months and possibly throughout the year. Pregnant females were observed in only three of the months sampled and a total of only eight embryos were recorded. Therefore, neither the date of conception nor parturition could be accurately determined. Although the disc width of the smallest free-swimming *H. walga* was 148 mm and that of the largest embryo was 80 mm, the disc width at birth is likely to be closer to the latter value as this species is far smaller than either of the other two dasyatids. Furthermore, since the functional ovary of a 153 mm female contained yolked oocytes and was thus maturing, birth must have occurred at a far smaller size.

Fecundity and maturity stages

The mean numbers of embryos (± 1 SE) per female of *D. zugei* and *H. walga* were 1.5 ± 0.24 ($n = 10$) and 1.4 ± 0.23 ($n = 8$), respectively, with a maximum of two embryos being present in the functional uterus. The functional uterus of pregnant females of *D. kuhlii* never contained more than one embryo ($n = 37$).

The presence of both pregnant and post-partum females of *D. kuhlii* in all of the months sampled except April (Fig. 3) provides further evidence that parturition occurs throughout all of those months, *i.e.* January to August. Mature, non-pregnant females, *i.e.* stage 3, were present in greater numbers than either pregnant or post-partum females, *i.e.* stages 4 and 5, in all months sampled. Stage 3 females constituted 57% of the total number of mature female *D. kuhlii*, compared with 29 and 14% by the latter two stages. Males at maturity stage 4, *i.e.* mature testes with seminal vesicles full of sperm, were found only in February and June, when they constituted *ca* 29 and 4%, respectively, of the total number of mature male *D. kuhlii* in those months (Fig. 3). Males at maturity stage 3 were present in all months sampled and constituted *ca* 93% of the total number of mature individuals.

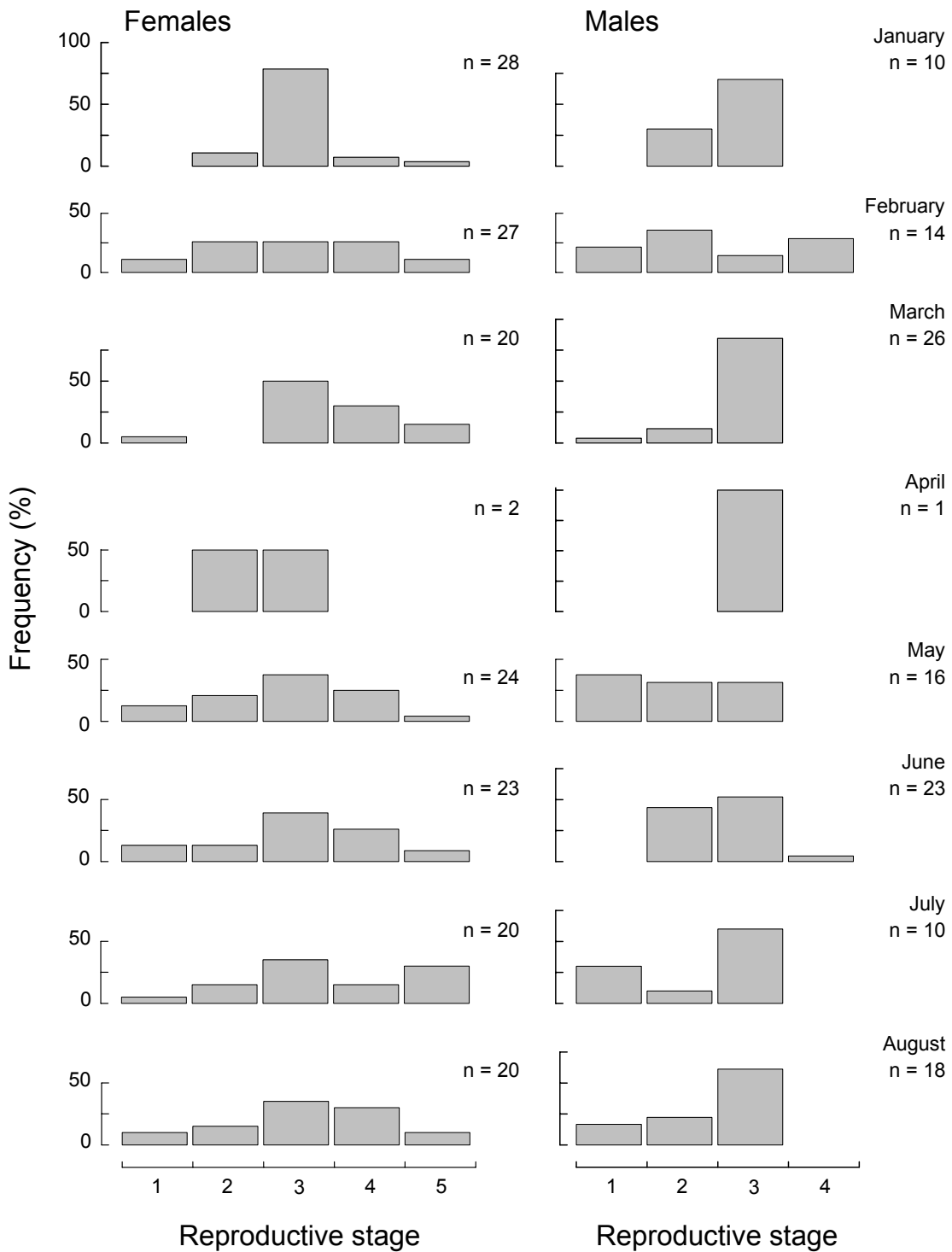


Figure 3 Monthly percentage frequencies of occurrence of sequential maturity stages of females and males of *Dasyatis kuhlii*.

Size compositions and size at maturity

A large size range of *in utero* female and male embryos of *D. kuhlii* were observed in each of the seasons sampled, which provides a further indication that this species does not have a seasonal reproductive cycle (Fig. 4). Only one recently-born individual, which had a disc width of 118 mm, was found. The disc widths of the majority of females lay between 240 and 319 mm, whereas those of most males lay between 220 and 279 mm (Fig. 4). The maximum disc widths of the females and males of *D. kuhlii* were 379 and 324 mm, respectively.

In utero females of *D. zugei* (20–79 mm DW) were recorded in both March and May and in June to August, whereas *in utero* males of this species (20–39 mm DW) were recorded only in March and May (Fig. 5). The majority of new-born females and males were recorded in June to August. The disc widths of post-partum females and males of *D. zugei* ranged from 104 to 271 mm and 112 to 211 mm, respectively (Fig. 5).

In utero embryos of *H. walga* were recorded in June to August, with disc widths of *ca* 2 mm, and were represented by larger embryos in March and May, with disc widths of 37–80 mm (Fig. 6). No new-born individuals of this species were recorded. The disc widths of post-partum females and males of *H. walga* ranged from 148 to 221 mm and from 156 to 212 mm, respectively, and reached maxima of 221 and 212 mm, respectively (Fig. 6).

The disc widths of the smallest mature females and males of *D. kuhlii* were 230 and 206 mm, respectively. Maturity was attained by all females by the time the disc width had reached 260 mm and by more than 90% of males by the time the disc width had reached 240 mm. The DW_{50s} for females and males of *D. kuhlii* at maturity were 237 and 239 mm, respectively (Fig. 7). The smallest mature females and males of *D. zugei* were 188 and 163 mm disc width, respectively. All females and males were mature by the time their discs

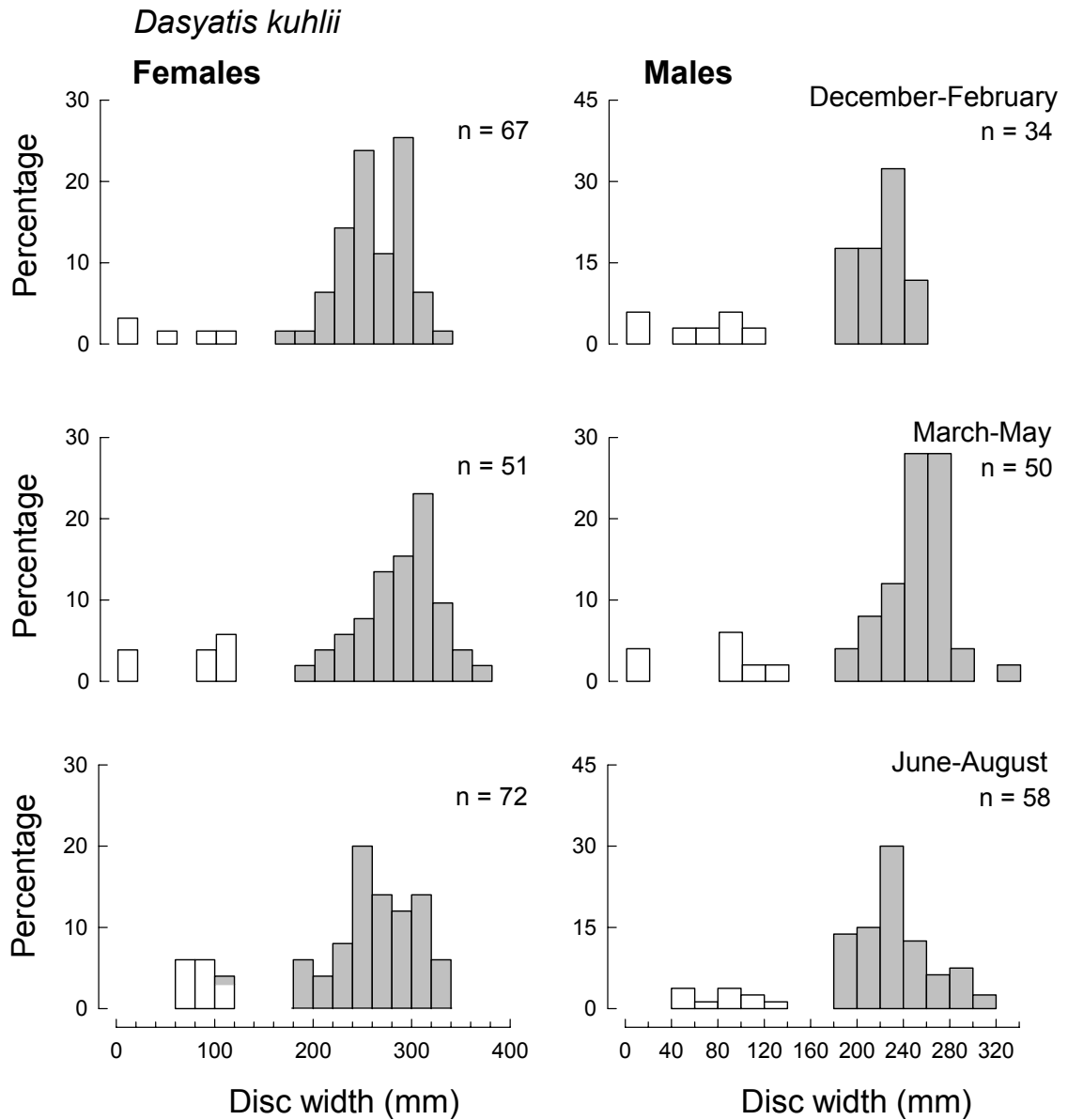


Figure 4 Disc width-frequency histograms of females and males of *Dasyatis kuhlii*. In this fig. and figs 5 and 6, white bars denote *in utero* individuals and grey bars denote postnatal individuals.

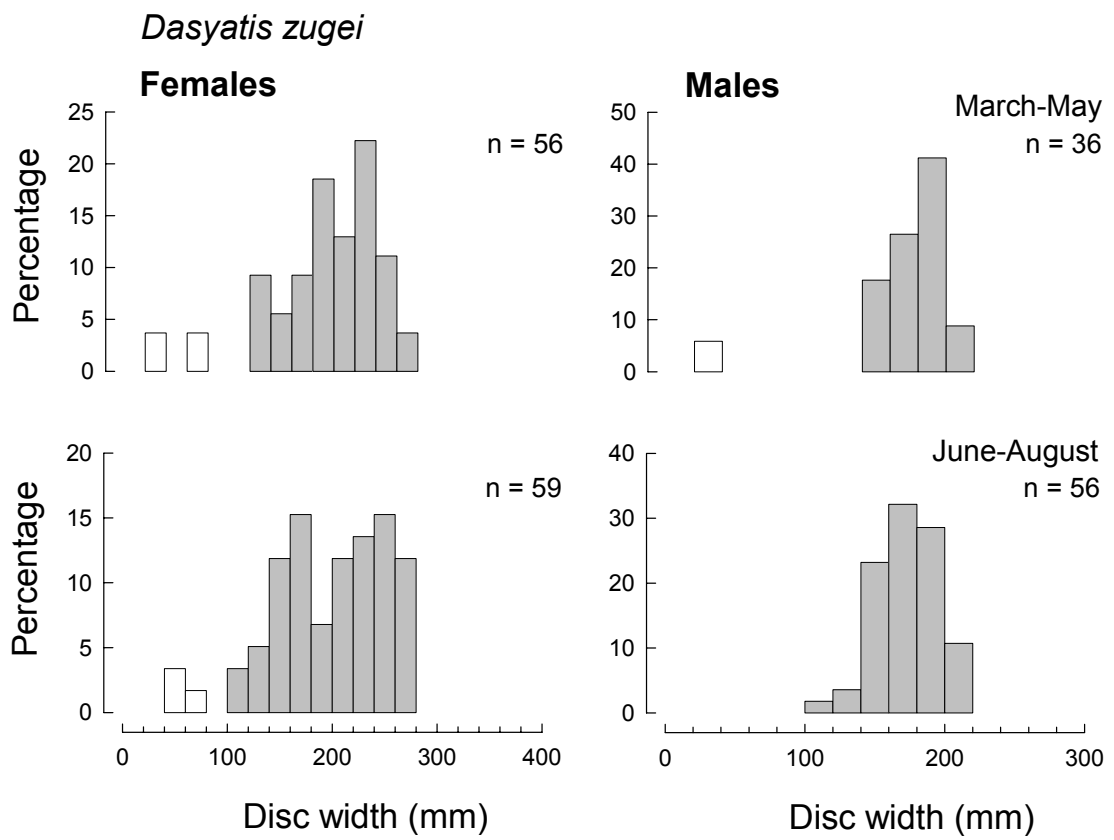


Figure 5 Disc width-frequency histograms of females and males of *Dasyatis zugei*.

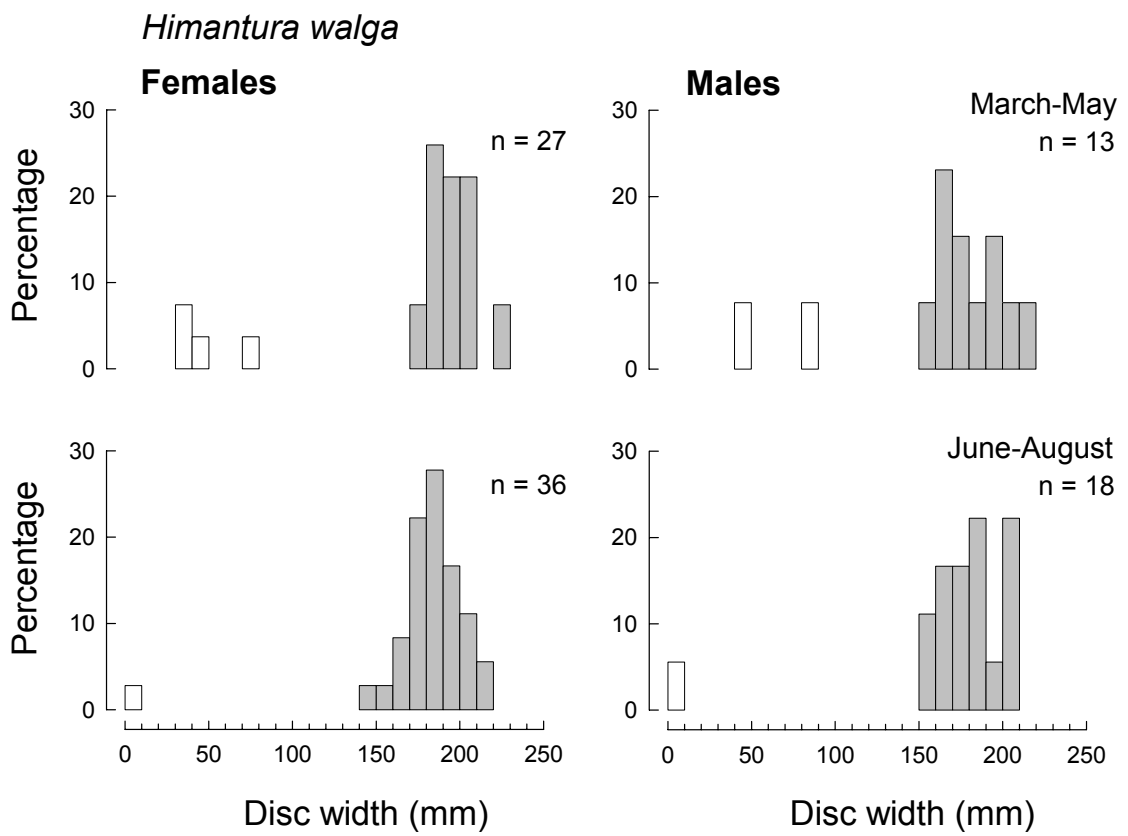


Figure 6 Disc width-frequency histograms of females and males of *Himantura walga*.

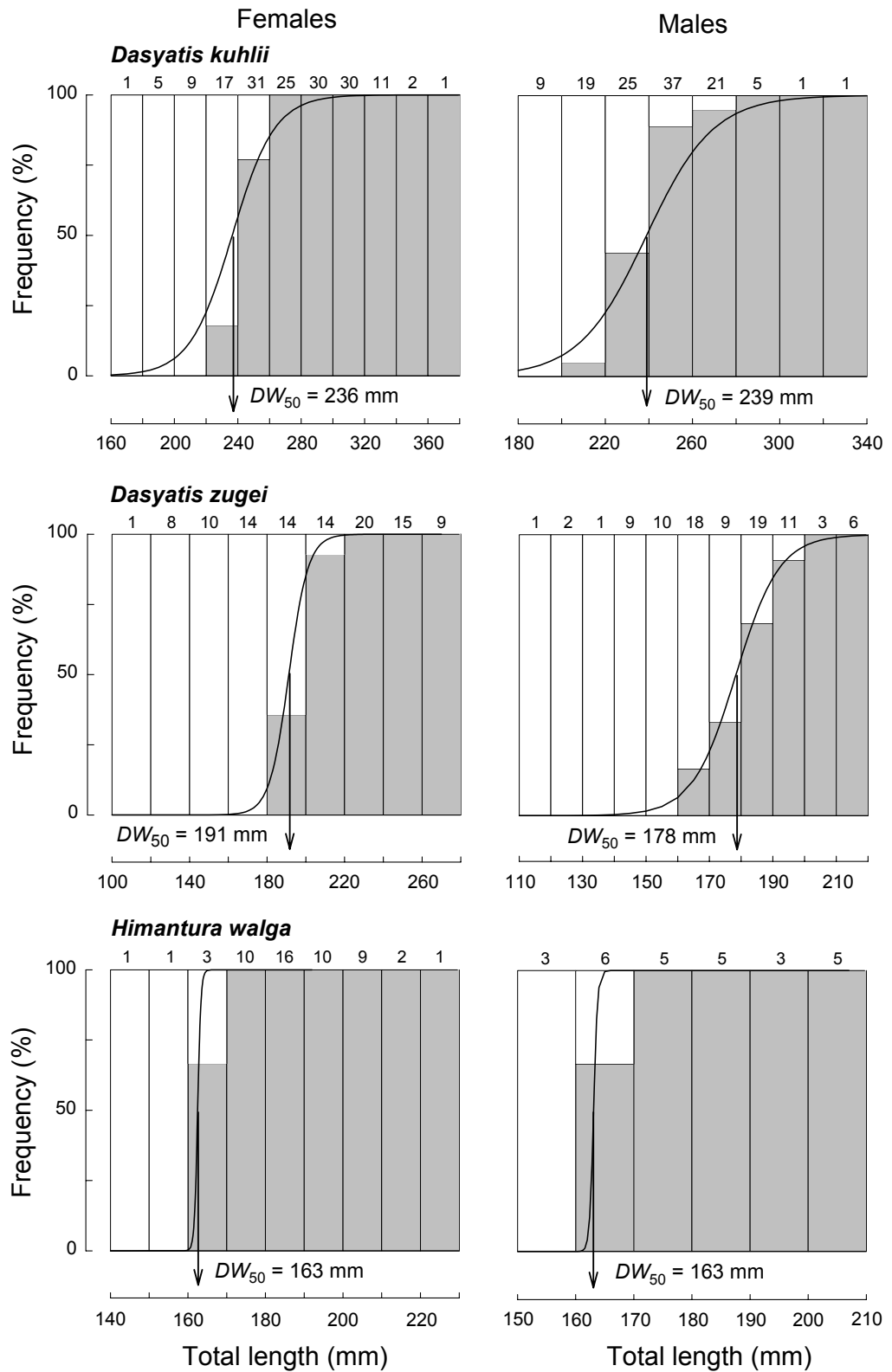


Figure 7 Percentage frequency of occurrence of immature, *i.e.* stages 1 and 2 (white bars), and mature, *i.e.* stages 3–5 (grey bars), in each sequential disc width class of female and male *Dasyatis kuhlii*, *Dasyatis zugei* and *Himantura walga*. Arrows indicate DW_{50} .

had reached widths of 220 and 200 mm, respectively. The DW_{50s} for females and males of *D. zugei* at maturity were 191 and 178 mm, respectively (Fig. 7). The smallest mature female and male of *H. walga* both had disc widths of 162 mm and all females and males had attained maturity by the time their discs had reached a width of 170 mm. The DW_{50s} for females and males at maturity were 162 and 163 mm, respectively (Fig. 7).

Age and growth of Dasyatis kuhlii

The mean monthly marginal increments on the vertebral centra of *D. kuhlii* with two or more translucent zones rose from 0.59 in January to 0.70 in March and then declined progressively to 0.49 in August (Fig. 8). Although the above trend suggest that the translucent zones may be deposited annually, samples need to be collected for the last part of the year, *i.e.* September to December, to confirm whether the monthly marginal increments follow a trend consistent with the annual deposition of a single translucent zone. Since it was not possible to determine either the date of conception or parturition for *D. kuhlii* (see earlier), the age at which the first translucent zone was laid down could not be determined.

The von Bertalanffy growth curve provided an adequate description of the disc widths vs the number of translucent zones for females and even more particularly the males of *D. kuhlii* (Figs 9a, b; Table 1). The growth coefficient (k) was substantially less for females than males, *i.e.* 0.311 vs 0.831, respectively, whereas the DW_{∞} was far greater for females than males, *i.e.* 313 vs 257 mm, respectively (Table 1). The maximum numbers of translucent zones recorded on the vertebral centra of female and male *D. kuhlii* were 15 and 10, respectively.

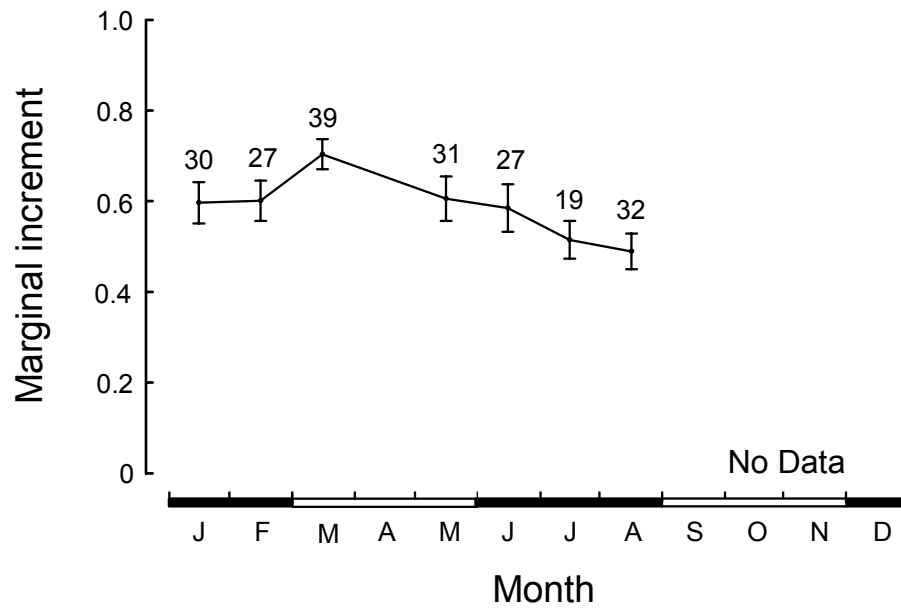


Figure 8 Mean monthly marginal increments (± 1 SE) for vertebral centra with two or more translucent zones. Samples size for each month is given. Marginal increments are recorded as a proportional value.

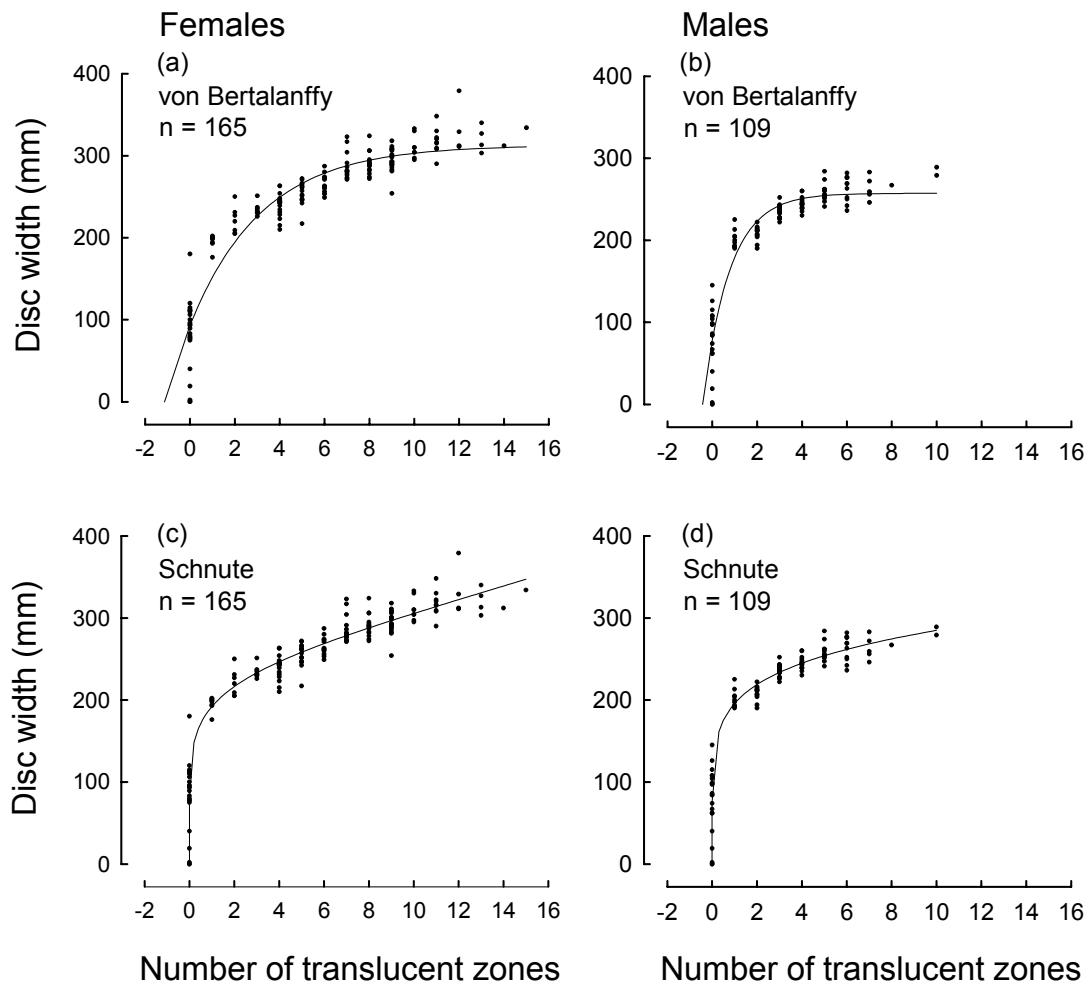


Figure 9 von Bertalanffy (a, b) and Schnute (c, d) growth curves fitted to the disc widths vs number of translucent zones for females and males of *Dasyatis kuhlii*. The parameters for the von Bertalanffy and Schnute growth equations for both sexes are provided in Table 1 and 2, respectively.

Table 1 von Bertalanffy growth parameters for females and males of *Dasyatis kuhlii*, including upper and lower 95% confidence limits, derived from disc widths vs number of translucent zones present in the centra of each individual. DW_{∞} , asymptotic disc width; k , growth coefficient; t_0 , hypothetical number of translucent zones at disc width zero; R^2 , coefficient of determination; n , sample size.

		von Bertalanffy parameters				
		k (year ⁻¹)	DW_{∞} (mm)	t_0	R^2	n
Females	Estimate	0.311	312.8	-1.13	0.889	165
	Upper	0.361	323.1	-0.88		
	Lower	0.261	302.4	-1.38		
Males	Estimate	0.831	257.3	-0.43	0.898	109
	Upper	0.997	265.1	-0.32		
	Lower	0.664	249.5	-0.55		

The Schnute growth curve significantly improved ($P < 0.001$) the fit of the disc widths vs number of translucent zones in the case of both sexes, by overcoming deficiencies at the lower and upper ends of the curves (*cf* Fig 9a-d). The improvement in the fit obtained by using the Schnute growth curve is emphasised by the resulting increase in the coefficient of determination (R^2) from 0.889 to 0.922 for females and from 0.898 to 0.915 for males (Tables 1, 2). Inadequacies in the fit to the lower end of the range in translucent zones by the von Bertalanffy growth curve for females, and to a lesser extent for that of males, is reflected in the “age” at zero disc width (t_0) being considerably less than zero, *i.e.* -1.13 and -0.43, respectively (Table 1). In contrast, the “ages” at which the Schnute growth curve intercepted the x-axis, *i.e.* equivalent to the t_0 , for females and males were very close to zero, *i.e.* -0.004 and -0.003, respectively. In the case of females, the Schnute growth curve passed upwards and over the von Bertalanffy growth curve to produce a maximum difference of 18.3% at one translucent zone, before passing back below that curve to produce a difference of only 3.0% at five translucent zones and then

rising again above that curve to produce a maximum difference of 23.3% at 15 translucent zones. In the case of males, the Schnute growth curve followed the same trend, producing maximum differences of 10.0, 2.4 and 10.1% at one, four and ten translucent zones, respectively.

The von Bertalanffy and Schnute growth curves both differed significantly ($P < 0.001$) between the sexes.

Table 2 Schnute growth parameters for females and males of *Dasyatis kuhlii*, including upper and lower 95% confidence limits, derived from disc widths vs number of translucent zones of individuals. DW_1 and DW_2 are disc widths at selected reference ages τ_1 (3) and τ_2 (12 in females, 8 in males) years; a and b are constants (both $\neq 0$); R^2 , coefficient of determination; n , sample size.

		DW_1 (mm)	DW_2 (mm)	a	b	R^2	n
	Estimate	233.0	322.3	-0.130	6.36	0.922	165
Females	Upper	238.3	330.3	0.011	8.78		
	Lower	227.7	314.3	-0.271	3.94		
	Estimate	233.6	274.5	-0.011	6.26	0.915	109
Males	Upper	239.3	286.5	0.325	10.10		
	Lower	228.0	262.4	-0.347	2.42		

Discussion

Reproductive biology of the three dasyatids and comparisons with other species

Since neither the ovulation nor parturition of *Dasyatis kuhlii*, *Dasyatis zugei* and *Himantura walga* occur in a particular well-defined period, the reproductive cycles of these species do not follow a clear seasonal trend. It was thus not possible to determine either the gestation period or the number of pregnancies per year for any of the three species. The gestation periods of dasyatids vary from 3 to 11 months (see Table 3). The gestation periods of the three species that occur in subtropical regions and for which this variable has

been determined, *i.e.* *Dasyatis sabina*, *Dasyatis sayi* and *Dasyatis guttata*, are far shorter than that of *Dasyatis centroura*, which occurs in temperate waters (Table 3). These differences are consistent with the data that have shown that water temperature can influence the rate of development of batoids. For example, the gestation period of the clearnose skate *Raja eglanteria* lasts about three months in the temperate waters of Delaware Bay and about two months in subtropical waters in Florida (Libby & Gilbert, 1960). A similar situation was found with the nervous shark *Carcharhinus cautus*, in which gestation lasts for 11 months in the subtropical waters of Shark Bay, but for only 8–9 months in the tropical waters of Darwin Harbour (see Chapter 5 and Lyle, 1987). Since *D. kuhlii*, *D. zugei* and *H. walga* live in tropical waters, they are likely to have relatively short gestation periods.

The fecundities of *D. kuhlii*, *D. zugei* and *H. walga*, *i.e.* litters of only one in the first species and 1–2 in the second and third species, are low even for an elasmobranch. The other dasyatids have higher fecundities, *i.e.* litters of up to six, which is presumably related to their larger size (Table 3). However, although the maximum disc widths of *D. kuhlii*, *D. zugei* and *H. walga* are far less than that of *Dasyatis guttata*, *i.e.* 221–379 vs 1020 mm for females, their sizes at birth were only slightly less than that of *D. guttata* (Table 3). This also helps account for the greater fecundity of the latter species.

The females of *D. zugei* reach maturity at a greater size than their males, which parallels the situation for the majority of dasyatid species and most elasmobranch species in general (Last & Stevens, 1994; Table 3). However, the females of both *D. kuhlii* and *H. walga* matured at similar sizes to their males, as is also the case with *D. sabina*

(Table 3). Since the reproductive parameters of a particular species vary among regions, it is informative to compare biological data for populations from throughout the range of a species. In the case of *Dasyatis centroura*, the individuals in the population in the south-eastern region of the United States are both born and mature at far larger sizes and reach greater body sizes than those of individuals in the population in Tunisia (Table 3).

The exploitation of dasyatids in the Indo-West Pacific, and in particular south-east Asia, is the highest in the world (Carpenter & Niem, 1998, 1999; Stevens *et al.*, 2000). However, the reproductive data obtained for the three species of dasyatids in the present study are the first recorded for rays in south-east Asia. This study represents the first step in the acquisition of the type of biological data which, together with catch and effort data, can be used to undertake risk assessments to determine which elasmobranch species are most at threat.

Age and growth of Dasyatis kuhlii

The only published data on age and growth of a dasyatid species were those derived for *Dasyatis pastinaca* in the eastern Mediterranean (Ismen, 2003). However, these data were based on only 49 vertebral counts and there was no validation that the growth zones were formed annually.

The mean monthly marginal increments on the vertebral centra increased from January and February to March and then declined progressively to August, when water temperatures would be expected to be least, indicating that the translucent zones on these centra of the females and males of *D. kuhlii* may be deposited annually (see Fig. 8). However, samples are required for the latter part of the year, *i.e.* September to December, to confirm that translucent zones are formed annually. Since neither conception nor parturition occurred during a particular time of the year, it was not possible to estimate the

precise age at which the first translucent zone is deposited and thus calculate the age at capture for individuals of *D. kuhlii*. Unfortunately, there has been no published report of attempts to validate that the translucent zone of any dasyatid species is deposited annually.

Although the von Bertalanffy growth curve provided a reasonably description of the disc width vs number of translucent zones data for females and males of *D. kuhlii* (cf Figs 9a, b), the Schnute growth curve provided a significantly better fit ($P < 0.001$) to those data (cf Figs 9c, d). This parallels the situation with two other ray species, *i.e.* *Trygonoptera personata* and *Trygonoptera mucosa* (White *et al.*, 2002) and the nervous shark *Carcharhinus cautus* (see Chapter 5), for which the Schnute growth curve generally provided a better fit than the von Bertalanffy curve to the size at age data. Although it is desirable, whenever possible, to use the von Bertalanffy rather than the Schnute equation as it is simpler and enables comparisons to be made with other elasmobranch species, the improvement to the fit of the disc widths at age of *D. kuhlii* by the Schnute growth curve was substantial, *i.e.* maximum difference between the disc widths at the various number of translucent zones, as derived from the two curves, was as great as 23.3%. The difference between the two growth curves was greatest at the upper end of those curves for both females and males, which accounts for the far lower estimates derived for asymptotic disc width (DW_{∞}) when employing the von Bertalanffy equation. Thus, the use of the estimates of both the above parameter and the growth coefficient (k) in the Pauly (1980a) equation for estimating the natural mortality of a species would generate very poor estimates for *D. kuhlii* and could subsequently result in poor management decisions.

In summary, this study represents the first detailed investigation of the biology of any dasyatid species occurring in south-east Asia. Each of the three species for which data were obtained, *i.e.* *D. kuhlii*, *D. zugei* and *H. walga*, and are caught in substantial quantities by commercial fisheries in Indonesia, had a reproductive cycle with no distinct seasonal

pattern. This study also represents the first attempt to determine the age of individuals of the most abundant of these rays, *i.e.* *D. kuhlii*, and to age individuals of any dasytid species occurring in the Indo-West Pacific.

The references cited in Appendix I and II are presented in the main reference section of my thesis.