

communication) and barramundi which consume primarily banana and "school" prawns (*Penaeus* and *Metapenaeus* spp.). Both *Telescopium* and banana prawns are known to consume directly some mangrove detritus (Robertson et al., 1992).

The cross-shelf connectivity of such fluxes are very difficult to measure, occur at a variety of spatial and temporal scales, and may be highly significant. For example, green turtles that feed on *Halodule* and *Halophila* seagrass in coastal bays and estuaries (Brand-Gardner et al., 1999) migrate seaward across the entire shelf to lay eggs at major outer-shelf rookeries in the northern and southern GBR (Limpus et al., 1992). At Moulter Cay, several hundred pairs of Nankeen night herons (*Nycticorax caledonicus*) nest and rear young, feeding principally on turtle hatchlings. Enough adult turtles die on the cay beaches to attract seasonal aggregations of tiger sharks (*Galeocerdo cuvieri*) to feed on the carcasses that float off from the inter-tidal. It is unknown if these aggregations of prey, predators, and scavengers occur on some rhythm or cycle to coincide with turtle nesting or only by local attraction through scent plumes or other cues. Nevertheless, this annual event provides a direct link between the inter-tidal and nearshore seagrass beds and outer-shelf reefs.

These links are trans-oceanic for some taxa. Feeding-ground captures of green and loggerhead turtles (*Caretta caretta*) tagged while nesting at eastern Australian rookeries over a 21-year period were summarised by Limpus et al. (1992) and Bowen et al. (1995). These turtles nest in the GBR region but range widely throughout the Arafura and Coral Seas. Tag recoveries included many from turtles that live in neighbouring countries and migrate to breed in Australia. The breeding females show a remarkable fidelity to home feeding grounds as well as to nesting beaches.

Aggregations of other "megafauna" occur in the GBRWHA in aggregation with seasonally or episodically abundant prey, including whale sharks (*Rhincodon typus*) in the Coral Sea "hotspot," which are encountered in October and November in association with an abundance of spawning lantern fish (*Diaphus* spp.) (Gunn et al., 1992; Wilson et al., in press). Yellowfin (*Thunnus albacares*) and bigeye tuna (*T. obesus*) aggregate at the same time and place and feed almost exclusively on *Diaphus* spp. there (McPherson, 1991).

A variety of migratory waders and seabirds also rely on the GBRWHA for overwintering and feeding grounds (Hulsman et al., 1997). These include several species which move north from Antarctica, such as the Wilson's storm petrel (*Oceanites oceanicus*) (Simpson & Day, 1993). Seabird feeding at sea and defecation at rookeries produce important accumulations of guano, providing one of the few feedback mechanisms, other than plate tectonic activity, for returning phosphorus to the land (E. Gyuris, personal communication).

Pisonia trees have root mycorrhiza with a unique adaptation to thrive in guano, and are major colonisers of sand cays in the southern GBR. In connection with movements of at least 18 species of seabirds the trees are spread long distances when the very sticky seeds adhere to their feathers (Walker, 1991). Similar, cross-shelf recruitment of rainforest trees to some northern GBR islands occurs when Torresian Imperial Pigeons (*Ducula spilorrhoa*) feed on the mainland and fly offshore to roost (King, 1990).

CONNECTIVITY AMONGST HABITATS THROUGH LARVAL DISPERSAL AND ONTOGENETIC MIGRATION

A long-standing idea predicts that dispersal is adaptive in environments subject to sudden unpredictable change (such as high sea level reefs in the cyclone belt), because given enough time all populations of non-dispersers go extinct. A wide variety of fauna and flora have dispersive larvae, seeds (seagrasses), or propagules (mangroves) which connect habitats across water bodies, but just how far these "juveniles" normally travel from their natal area is an unanswered question in marine biology (Jones et al., 1999).

Sometimes extreme physical gradients are crossed, as in the case of eels (*Anguilla australis*, *A. obscura*, and *A. reinhardtii*), which are spawned in the oceanic waters of the Coral Sea (Merrick & Schmida, 1984) but migrate as elvers into the uppermost water bodies in catchments—sometimes overland in wet grass. "Supply-side ecology" (Caley et al., 1996), "source-sink" modelling (Dight et al., 1990a and b), and the "recruitment-limitation" hypothesis (Doherty & Williams, 1988) have been major research themes addressing this major difference between "open" marine and "closed" terrestrial ecosystems.

In the case of reef fish, Doherty et al. (1985) took the view that the "adaptive-ness" of larval dispersal is selected for in the patchy pelagic environment of the GBR water column. This followed observations that fish larvae must have available in close proximity a relatively high density of appropriately sized food organisms for survival. These densities are only observed in smaller-scale patches, on the order of metres or less, and in turn these patches are themselves part of larger patches or production systems, whose upper dimensions may be on the order of tens of metres to hundreds of kilometres (Williams & English, 1992). The problem of placing eggs (or larvae) into an appropriate (pelagic) environment is the life's work of a fish. This reasoning could be applied equally well to larval retention around oceanic island reefs, given that coastal waters there are more productive than the nutrient-depleted oceanic environment.

Early attempts at understanding dispersal had approximated larvae as passive particles, but Stobutzki and Bellwood (1997 and 1998) showed remarkable swimming and sensory abilities of a range of reef fish larvae, to "hold" favourable position in the pelagic environment and seek out settlement sites on reefs. For example, surgeonfish juveniles (Acanthuridae) were able to swim, on average, for 194.3 h continuously, covering the equivalent of 94.4 km, and distances covered by other taxa ranged from 8.3 to 62.2 km. The late pelagic stages of reef fish also display nocturnal orientation behaviour, possibly in response to sound, which may aid in their settlement on reefs.

Most recently, these abilities have been recognised in tests of "self-seeding and larval retention" hypotheses (see Johannes, 1978) in explaining replenishment of offshore (and oceanic) island reefs. Jones et al. (1999) employed direct mark and release of over 10 million damselfish embryos to demonstrate the self-recruitment of a Lizard Island species. Swearer et al. (1999) used trace element and growth rate

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truncatus), tunas, and sharks, and pursued from above by diving brown booby birds (*Sula leucogaster*) and frigate birds (*Fregata minor*). Studies of the multi-species aggregations showed that northern pilchards (*Amblygaster sirm*) and golden-lined sardines (*Sardinella gibbosa*) were major components, together with small, fusiform carangids and scombrids (*Selaroides leptolepis*, *Decapterus russelli*, *D. macrosoma*, *Rastrelliger kanagurta*, *Cybiosarda elegans*) (Cappo, 1995a and b). Northern pilchards and sardines occurred in 85% of black marlin stomachs, and comprised 93% of prey items. Sailfish diets were more varied, including larval triggerfishes and leatherjackets, but the northern pilchard occurred in 57% of the sailfish examined. Later in summer (see Figure 8) the adult pilchards and sardines were detected in smaller schools and were generally very large, suggesting that they were the old remnants of the winter population. The predators on the grounds were also different, with small numbers of migrating spotted mackerel (*Scomberomorus munroi*) appearing, and with surface activity being dominated by schools of tuna (*Thunnus tonggol* and *Euthynnus affinis*) feeding on small, juvenile northern pilchards and other fish larvae.

The birds above the fish-feeding activity also changed to abundant flocks of several species of terns, including the little tern (*Sterna albifrons*) and the crested terns (*S. bergii*, *S. bengalensis*). Later, in autumn, large numbers of Spanish mackerel in the 5- to 9-kg range were seen on the grounds. By June or July, the schools of small black marlin (15 to 40 kg) usually arrived in numbers, but each year was different in terms of timing of arrival, numbers, and size. These seasonal changes in bait, birds, and billfish are generally best explained by the changeover periods from southeast trade winds bringing cooler water in April, to the northwest monsoons in October bringing down warmer waters from the north.

The prevailing hypothesis is that the bays adjacent to the GBR lagoon billfish grounds are exceptional nursery areas for baitfish and, as they grow, these fish migrate progressively out to the grounds (Williams & Cappo, 1990). An abundance of suitable food for these early life history stages has been documented in the shallow bays, especially near mangrove river mouths, in the form of zooplankton (McKinnon & Klumpp, 1998a and b; Robertson et al., 1988; Williams et al., 1988). Aerial survey in summer 1990 over the four major capes in the Central GBR spotted over 320 schools of juvenile baitfish along a 230-km stretch of coast. Over 90% of these schools were aggregated around river mouths, but a key uncertainty concerns the role of mangrove crab zoeae in the diets of these fish.

Pulses of juvenile golden-lined sardines appeared within 100 m of shore in October to December in Bowling Green Bay, and by April had moved offshore into deeper bay waters toward the billfish grounds. During April to May, the sub-adult sardines were passing the Cape Bowling Green sand spit, and by September they were in spawning condition on the billfish grounds (Williams & Cappo, 1990; Cappo, 1995a). These nearshore schools of juvenile sardines and pilchards are heavily preyed upon by grey mackerel (*Scomberomorus semifasciatus*) and other fish and sharks (Simpfendorfer, 1998) around pinnacles and rocky headlands. The northern pilchard showed a much different life cycle to the sardines and all life stages of the pilchards—from larvae to juveniles, sub-adults, and spawning adults—were found offshore in the vicinity of the billfish grounds.

CONCLUSION

The conventional "coral reef paradigm" highlights nutrient trapping and recycling and close co-evolution of species in symbiotic and commensal relationships to accumulate biomass in otherwise nutrient-poor tropical oceans. This has encouraged a popular view of reefs as somewhat self-contained biological islands, which are linked through episodes of larval dispersal with other reef systems. Our conceptual model extends this to reflect current appreciation of the GBRWHA as a profoundly interconnected system in which the non-reef communities are important "load bearing" elements in terms of the integrity and health of the larger system. The extent and nature of the seaward influence of human activities in the coastal plains and fringe are under study, but understanding is complicated by the nature and connectivity of natural disturbances. Clear gradients and links can readily be shown between biotopes, in "places, processes, and protein," but the strengths of these links and the implications of their disruption are not yet sufficiently known to fully predict human impacts. Landscape-scale research and management of the GBRWHA is needed, especially in the poorly known "inter-reef" and through the coastal fringe into the catchments.

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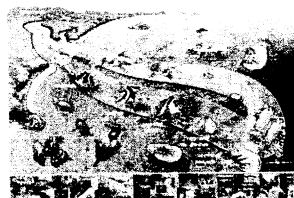


FIGURE 1 Schematic overview of the biotopes of the GBRWHA from "range to reef," showing episodic nutrient inputs from catchments and Coral Sea upwelling, and a generalised life cycle of a tropical snapper (the red emperor *Lutjanus sebae*.)

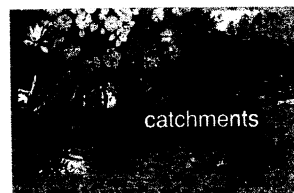


FIGURE 2 Montage from coastal plain aquatic environments, featuring a juvenile barramundi (*Lates calcarifer*) and long-finned eel (*Anguilla reinhardtii*) which move between marine and freshwater environments.



FIGURE 3 Montage from tidal estuaries featuring mangrove forests and the shelter offered by prop roots and turbid waters. The mud crab *Scylla serrata* feeds and burrows in mangrove creeks and females migrate to the outer continental shelf to spawn.



FIGURE 4 Montage from seagrass communities which trap sediments and provide nursery habitats for a wide range of invertebrates and fish. Several seagrass species are grazed by dugong (*Dugon dugon*) (featured) and green turtles (*Chelonia mydas*).

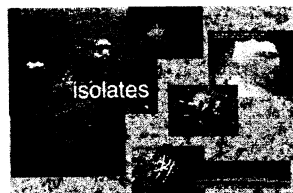


FIGURE 5 Montage typical of the patchy "isolates" known from the continental shelf. Isolates vary from small patches of benthos on soft sediment to larger clusters of "megabenthos" on "hard ground."



FIGURE 6 Montage from "inter-reef gardens," arbitrarily differentiated from "isolates" by a prevalence of filter feeders (e.g., gorgonians and sponges) aligned by currents.

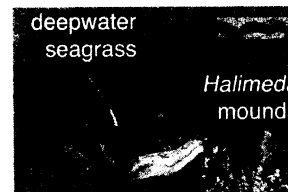


FIGURE 7 Montage of deep water seagrass and *Halimeda* bioherms recently discovered to cover thousands of square kilometres on the mid- to outer shelf in the GBRWHA. Upper right image shows echosounder trace of *Halimeda* mounds with an amplitude of several metres. An aerial perspective of discrete mounds tens of metres across is shown at lower right.



FIGURE 8 Schematic cycles in movement of baitfish and predators off Cape Bowling Green in the central section of the GBR. Colour coding of arrows indicates time of year, from winter (colder blue) to summer (hotter orange/pink).