11 Connectivity in the Great Barrier Reef World Heritage Area— An Overview of Pathways and Processes

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INTRODUCTION

The notion of landscape-scale ecosystem "connectivity" is neither new nor a wholly scientific construct. Australian poet Judith Wright summed up what many scientists intuitively feel about reefs when she wrote:

> Biologists now often talk of the Reef as only the main system of an overall system of reefs throughout the whole Indo-Pacific region, and suspect that there may be interconnection of all these reefs through the planktonic movement across the ocean. The Reef cannot be thought of, either, as separate from the mainland coasts, with their many fringes of great mangrove forests that form a tremendously fertile breeding-ground for

many species which during part of their lives may enter the waters of the reef proper. The interlocking and interdependent physical factors which have so long kept the reef alive and growing, such as water temperatures, freshwater replenishment from streams and estuaries, the tidal movements which bring deep ocean water in and out of the calmer and narrower waters within the Barrier, and the winds and weather systems, are probably all indispensable to the maintenance and dynamics of its living species. (Wright, 1977)

A broad knowledge base is associated with the Great Barrier Reef (GBR) province from the earliest navigational survey vessels of the 1800s, subsequent scientific expeditions, and an expanding body of contemporary research literature from the physical, geological, ecological, and molecular sciences. This has been complemented by an important body of unpublished literature and personal observations collected from the public and reef users, making the GBR one of the most comprehensively investigated ecosystems on earth. Across these disciplines "connectivity" is a recurrent theme, and here we give an illustrated overview and examples of some types and scales of ecological connectivity spanning the GBR World Heritage Area, with an emphasis on fish life-history studies.

THE GREAT BARRIER REEF IN TIME AND SPACE

Geological investigations of the GBR have revealed a "layer cake" cap of modern (9000 years to present) limestone to overlie an ancient (last interglacial ~120,000-year-old) body of reefal limestone. This is evidence for a previous incarnation of the GBR during a past era of high sea level (Davies & Hopley, 1983). In essence the GBR is only a living ecosystem during phases of high interglacial sea level, for periods less than 10% of the last 500,000 years (Potts, 1984).

The GBR does not exist as the living system we currently "know" during those intervals of time when conditions are rendered unfavourable for reef building on the continental shelf by falling ice-age sea levels (Davies, 1992). During these times the genetic legacy of GBR must, by inference, lie on the present continental slope or elsewhere in the western Indo-Pacific. The early closure during any ice age of the shallow Torres Straits seaway to the north of the GBR ensured that the Coral Sea was the principal connection in spread of larvae derived from inter-stadial reef communities.

The structure and dynamics of present-day GBR communities can be determined by processes operating in both evolutionary and ecological time and on both local and larger spatial scales (Bellwood, 1998; Caley, 1995; Veron, 1995). Palaeogeography determines the chance of an organism occurring at a particular location, and biological constraints and physiological tolerances (e.g., to salinity and temperature) will govern its spread and persistence. The genetic connectivity of populations can occur at the larger of these scales across oceans and is shaped by sea level changes and formation of physical barriers to dispersal (Veron, 1995; Williams & Benzie, 1998). Connectivity is visible at progressively larger scales in reef ecosystems, from the inter-cellular level between coral polyps and zooxanthellae, to symbioses and commensalism amongst species (e.g., Poulin & Grutter, 1996), to tight nutrient capture

and recycling in food webs on coral reefs (Hamner et al., 1988; Alongi, 1997). Here we focus on the mesoscale ecological processes and pathways.

A WALK AROUND THE GREAT BARRIER REEF WORLD HERITAGE AREA

The Great Barrier Reef World Heritage Area (GBRWHA) does not extend to the coastal plain. However, for this review we broadly define primary habitats, or "biotopes" linked to the health and integrity of the GBR system, to be catchments and coastal floodplains, estuaries and bays, shallow and deepwater seagrass beds, lagoonal and inter-reef "gardens and isolates" of megabenthos, coral reefs, and the pelagic realm that links them all.

The general ecological framework for the pathways discussed in this chapter are illustrated in the cross-shelf vista in Figure 1, with a representation of the life cycle of the red emperor *Lutjanus sebae*. This species is perhaps the most familiar to the public of the lutjanid family of fishes, which are known to make ontogenetic migrations (to various degrees) between biotopes. The montage of biotopes at the bottom of Figure 1, and Figures 2 to 7, summarise the habitats linked in some way to the ecology of the lutjanid family (and others) of fish.

Beginning upstream (Figure 2), aquatic species in freshwater wetlands from the coastal plain have evolved to exploit ephemeral habitats in seasonal or episodic monsoon flooding, during which spawning, upstream dispersal, and downstream migrations occur in association with pulses of primary and secondary production (Bayley, 1991). Fish, crustaceans, amphibians, reptiles, and piscivorous and herbivorous birds move about the landscape and between catchments by migrating upstream, downstream, or across floodplains and along riparian corridors.

Between these flood events the degree of shading and litter-fall from riparian vegetation has profound influence on stream temperatures, light regimes, and stream metabolism—the balance between primary production and respiration. Healthy streams are net consumers of organic carbon and respiration exceeds primary production, so oxygen concentrations are high (Bunn et al., 1999). Loss of shade and aquatic weed and pasture grass invasions cause tropical freshwater streams to flip to net production of carbon, high nocturnal plant respiration and bacterial oxygen consumption, and massive streambed accumulation of decaying matter and sediment in anoxic conditions (Bunn et al., 1997 and 1998).

The connectivity of disturbances from human uses and impacts is most evident in the coastal plain and fringes immediately behind the GBRWHA and above the natural, or artificial, restraints to saline intrusion (see State of the Environment Queensland, 1999 for reviews). For example, alteration of natural drying and filling cycles for some tributary lagoons of the Burdekin River has had some positive and negative effects on wetland birds and fish. Year-round filling has enabled introduced duckweed (*Cabomba caroliniana*) and water hyacinth (*Eichornia* spp.) to flourish and sometimes completely cover and de-oxygenate entire lagoons. The weed mats shelter introduced fish (e.g., *Tilapia, Oreochromis, Gambusia*) from native predators.

Introduced pasture grasses such as para grass (*Brachiaria muticum*) and hymenachne (*Hymenachne amplexicaullis*) have invaded the riparian zones and their runners over-grow the floating weed mats to form concentrated fuel loads for very hot wild fires. In turn, these fires kill remnants of riparian trees (e.g., *Melaleuca* spp., *Eucalyptus* spp.) and palms (e.g., *Pandanus* spp., *Livistona* spp.) that shaded and cooled the lagoons (J. Tait, personal communication).

Farther downstream, the landward advance and retreat of saline surface and groundwaters with drought, flood, and tide are a fundamental forcing in the dynam-ics of floodplain primary production, governing both the distribution and growth of ephemeral hydrophytes, bulkuru sedgelands (*Eleocharis dulcis*), and ti-tree (*Melaleuca* spp.) stands. The dramatic saline intrusion on the Mary River floodplain in the Northern Territory (Woodroffe et al., 1993) shows the rapidity of change in freshwater habitats and creek evolution with tidal influence. A similar advance of mangroves into freshwater ti-tree swamps has occurred in the Moresby catchment of the GBRWHA due to expansion of the tidal prism from the deepening of Mourilyan Harbour mouth (Russell et al., 1996). Both cases may exemplify the effect of rising sea levels.

The coastal fringe is a geologically young, dynamic zone of diversity, produc-tion, confusion, and conflict in the forces of nature, culture, and law. Lowlands bear-ing freshwater lagoons and swamps, salt-flats, marshes, and mangroves are buffered from sea waves and wind disturbance by dunes and beach ridges, estuaries, and semi-enclosed bays bearing headlands (Figure 3). Within catchments, slopes decrease toward the sea allowing the deposition and processing of sediments, minerals, and nutrients in low energy environments.

Vegetated habitats of the coastal plain and fringe, such as the *Melaleuca* swamps, sedgelands, mangrove forests, and seagrass beds (Figures 2 to 4), shelter many species between wet seasons and episodic flood events. They also serve to trap sedi-ments and nutrients and kick-start food chains (see Alongi, 1997; Bunn et al., 1999; Butler & Jernakoff, 1999; Cappo et al., 1998; Robertson & Blaber, 1992). The swamp habitats, in particular, are known for their effects on the residence time and passage of raw sediment and nutrients derived from catchments and have become known as the "kidneys of the coastal zone" (Crossland, 1998). Seagrasses also affect water movement over the beds of blade-like leaves, and settle and bind sediments (see Butler & Jernakoff, 1999). In general terms, the structural complexity of freshwater macrophyte fronds, mangrove prop roots, and seagrass blades provides shelter and protection for juveniles and their prey, substrata for attachment of palatable epi-phytes, and the bases of detrital food chains, as well as altering local hydrology (Wolanski, 1994).

The estuaries may loosely be defined as the zones where there is an interface, or "salt wedge" between fresh and salt surface waters—but the same interfaces also occur in groundwater in the poorly recognised "underground estuaries" (G. Brunskill, personal communication). Chemical reactions at the surface interface cause re-mineralisation, flocculation, and precipitation of nutrients and sediments (e.g., Woodroffe, 1992; Wolanski et al., 1992). Upwelling and river discharge account nearly equally for at least 75 to 80% of total nutrient inputs in the GBRWHA (see

reviews by Wasson, 1997; Rayment & Neil, 1997). Subterranean flow out into the areas between reefs is also known to occur at certain times and places, but this flux and the consequences of the nutrients it carries are unknown (P. Ridd, personal com-munication). Trawlermen report "wonky-holes" where (presumably) freshwater seeps up into lagoon waters. These are reported not to be active year-round, and can fill with sediment between outflow events.

Rainfall (or the lack of it) is a prime disturbance in the dynamics and connectiv-ity of coastal habitats and coral reefs. Flood pulse events naturally carry over into the estuarine zone, delivering freshwater, sediments, nutrients, and contaminants into the coastal zone, and triggering both downstream migration of catadromous fish and prawns to spawn and upstream return of larvae to reach nurseries. Catadromous species in the GBRWHA include the barramundi (*Lates calcarifer*), jungle perch (*Kuhlia rupestris*), tarpon (*Megalops cyprinoides*), eels (*Anguilla* spp.), and fresh-water prawn (*Macrobrachium* sp.) (Russell & Garrett, 1985). Bayley (1991) sug-gested that a "flood pulse advantage" is evident in the amount by which freshwater fish yield per unit area is increased by flood pulses in tropical fisheries, and that watercourses are more or less acting as refugia for native freshwater fishes between flood events when they can access floodplains (the "flood pulse concept"). The most visible effects of prolonged rainfall events occur in the supra-littoral saltpans nor-mally encrusted with thick layers of salt. These can become freshwater lagoons in which bulkuru and hydrophytes flourish from dormant seed or banks of underground corms. In turn, this primary production attracts migratory magpie geese (*Anseranas semipalmata*), black swans (*Cygnus atratus*), yellow spoonbills (*Platalea flavipes*), brolgas (*Grus rubicundus*), frogs (e.g., *Cyclorana novaehollandiae*), insects, fish, and crustacea to feed for various periods (see Australian Nature Conservation Agency, 1996).

The importance of the "environmental flows" of freshwater in estuaries is poorly studied (Loneragan & Bunn, 1999). Most widely cited are significant positive or neg-ative correlations between rainfall, salinity, and river discharge for banana prawns (*Penaeus merguiensis*) in some regions (see Staples et al., 1995 for review). Access to, and persistence and quality of, barramundi nursery habitats in supratidal fresh-water swamps are also enhanced by episodically high rainfall, sufficient to produce recognisable signals in the size structure of fishery landings 3 to 4 years after the event (R. Garrett, personal communication).

The physiology of osmoregulation is limiting at lower temperatures (Dall, 1981), so the maintenance of a narrow salinity/temperature balance is not so critical in the tropics, enabling aquatic fauna to cope well with estuarine salt wedges, whereas the wedge profoundly influences the distribution of temperate species. Surprisingly, there has been little Australian use of such a fundamental concept (Cappo et al., 1998), but it fits well the generalisation that there is more plasticity in the life histo-ries of tropical species. For example, the giant trevally *Caranx ignobilis* and the big-eye trevally *C. sexfasciatus* are found in the tropical Kosi Bay estuary down to about 0.25 ppt—the bare minimum needed for kidney function—but temperature has to be at optimum level (Whitfield et al., 1981). The same species visit freshwaters of the north Queensland estuaries (V. McCristal, personal communication), and there is an

increasing awareness of the ability of our tropical serranids and lutjanids (and other families) to persist in low salinities (e.g., Sheaves, 1996). In contrast, no temperate carangids enter freshwater, major movement by temperate fish occurs downstream to escape freshwater flows in southern estuaries, and there are very few euryhaline species in the south.

Just offshore from the vegetated coastal fringe, the dominance of fine, terrigenous sediments has produced an "estuarisation of the shelf" (*sensu* Longhurst & Pauly, 1987) that offers alternative nursery habitats in turbid bays to the shelter and enhanced food supplies in estuaries. Sediment type is a major determinant of habitat type and fisheries production. In general terms the finer sediments have higher rates of benthic primary and secondary production with more benthic infauna available as food for prawns, crabs, fish, and other higher consumers (Alongi, 1997; Robertson & Blaber, 1992). Seagrass and algal beds in bays (Figure 4) also provide critical nursery habitat for tiger prawns (Loneragan et al., 1998), and are directly grazed by herbivorous dugong (*Dugong dugon*) and green turtles (*Chelonia mydas*) (Lanyon et al., 1989; Preen, 1995). More subtle, but perhaps equally important, is the indirect support to some coastal fishes and crustaceans given by seagrasses through food chains based on grazing on epiphytes and seagrass detritus (see reviews in Butler & Jernakoff, 1999; Watson et al., 1993). A "critical chain of habitats" may best explain the life history requirements of such species (Cappo et al., 1998) which include the juveniles of lethrinid emperors found as adults on coral reefs (Wilson, 1998).

Farther offshore, between the mainland and the mid-shelf reef matrix, lies the "GBR lagoon," a wide expanse (56 km in the central section) of shallow (15 to 40 m in the central section) water characterised by changes in sediments and biodiversity. Sediments nearshore in depths <15 m generally have high silt and clay fractions of terrigenous origins (Jones & Derbyshire, 1988), changing to carbonate-based facies around the 22- to 23-m isobaths (Birtles & Arnold, 1988). Within the lagoon are patchy assemblages or seafloor "isolates" of invertebrate megabenthos (Figure 5). Larger communities of these filter feeders develop in "inter-reef gardens" where directional currents are prevalent (Figure 6). *Halimeda* bioherms (Drew & Abel, 1988) and deepwater seagrass beds (Figure 7) occur in the shelf lagoon and between the emergent reefs and support poorly known resources of biodiversity (Lee Long et al., 1996). Also lying within the outer reef matrix are relatively large, unstudied areas of corals and other phototrophic reef-building organisms in depths <50 m (Birtles & Arnold, 1988).

These continental habitats are connected by flooding and outwelling of material from the coastal zone, through its food web extensions and by ontogenetic movements and migration of organisms. These fluxes vary on regular tidal and seasonal time scales, on less regular quasi-decadal, or longer, climate cycles (Lanyon & Marsh, 1995; Lough, 1998; Jones et al., 1998), and with irregular, intermediate, or catastrophic disturbances such as floods, cyclones, and "phase shifts" (see Done, 1992; Done et al., 1997; McCook, 1999; Preen et al., 1995; Puotinen et al., 1997).

Toward the mid- and outer-shelf the proportion of reef-related species found in inter-reefal habitats increases. Reef-derived sediments, rubble, and "hard grounds" become important sites for patch nucleation of inter-reefal bryozoans, ascidians,

sponges, corals, and crustose coralline algae, and the effect of reef structures on local tides and currents becomes an influence on the nature of seafloor communities. In turn, the skeleton-forming benthos of the lagoonal zone can provide settlement sites for colonial and solitary megabenthos, such as gorgonians and macro-algae. Farther offshore an "inter-reef" community of megabenthos can be recognised, on isolates or attached to Pleistocene surfaces and other areas of calcium carbonate rock pockmarked with solution holes and overlain by a veneer of carbonate sediment. These "natural isolates" and "megabenthos gardens" (see Figures 1, 5, and 6) of biological origin form "islands of hard substrata in a sea of otherwise unstable soft sediments" (Birtles & Arnold, 1988).

They provide the basis for the rise in diversity deeper than 22 to 23 m in the GBR lagoon. At shallower depths the isolates cannot form because of the frequent disturbance by surface wave action. This link between substratum type and sessile megabenthos may be a well-recognised feature of our tropical shelves (Long et al., 1995), but the role of seabed current shear stress in determining the patterns of distribution of isolates and patches is only now being investigated (Pitcher et al., 1999).

Large sponges (e.g., *Xestospongia, Ianthella, Cymbastella*), gorgonians (e.g., *Ctenocella, Subergorgia, Semperina, Echinogorgia*), the vase coral *Turbinaria*, and patches of macroalgae are characteristic features of the patches. These megabenthos shelter numerous commensal animals within their internal chambers, and other macrofauna, such as echinoderms, crustacea, and octopus, shelter within crevices beneath the megabenthos canopy (Hutchings, 1990; Pitcher, 1997). Hawksbill turtles (*Eretmochelys imbricata*) and some pomacanthid angelfish eat sponges. These diverse and poorly known communities have attracted significant research in pursuit of natural products of pharmaceutical promise (Hooper et al., 1998).

The provision of this structural complexity shelters a range of fish species which prey on the organisms living in the patches, or move away at night to consume softbottom invertebrates in the unconsolidated sediments nearby. These fish most notably include the commercially and recreationally important lutjanids, lethrinids, and serranids. For example, the "red snappers" (*L. sebae, L. malabaricus, L. erythropterus,* and *L. argentimaculatus*) (see Figure 1) and the "sweetlip emperors" (*Lethrinus* spp.) form the major part of the inter-reef line fishery on the GBR (Williams & Russ, 1994). Underwater video has shown the painted sweetlip (*Diagramma pictum*) to shelter from the current by sitting motionless inside the cups of large *Xestospongia* and *Turbinaria* spp. The isolates and megabenthos patches may also be very important as "stepping stones" for fish such as mangrove jack that move offshore across the lagoon to deeper habitats. The shelter and trophic roles of production in deep-water seagrass beds (Lee Long & Coles, 1997) and *Halimeda* bioherms (see Figures 1 and 7) are also very poorly known, although dugong are known to feed in the deepwater seagrass beds (W. Lee Long, personal communication).

Deep Coral Sea waters from far offshore also influence the GBR in two main ways (see Wolanski, 1994 for review). First, tidal "jetting" occurs in narrow passes separating shelf-edge reefs. This causes periodic local nutrient upwelling correlated with abundant growth and vast, mound-like seafloor accumulations (bioherms) of the calcareous algae *Halimeda* (Wolanski et al., 1988). Second, episodic intrusions of

high nutrient water move up the continental slope and inshore at a regional scale, stratifying the summer water column and influencing the abundance and production of phytoplankton communities. Blooms of the diatom *Trichodesmium* during this stratification can cause doubling of carbon fixation rates (Alongi, 1997).

THE CROSS-SHELF PARADIGM AND LAND-OCEAN PROCESSES—HOW FAR OFFSHORE DOES "LAND INFLUENCE" EXTEND?

A recent stock-take (Lucas et al., 1998) of the values and biodiversity of the GBR-WHA showed three common traits in major phyla of fauna and flora—very high diversity, a lack of knowledge for most groups, and cross-shelf changes in diversity and abundance. In that report, distinct reefal and inter-reefal faunas and nearshore communities were reported for the phytoplankton, the mangroves (37 species: Duke, 1992), the seagrasses (15 species), the *Halimeda* (Drew & Abel, 1988), the corals (>360 species: Veron, 1995), the octocorals (80 genera), the flatworms (>200 species), the molluscs (5000 to 8000 species), zooplankton (McKinnon & Thorrold, 1993), the echinoderms (Birtles & Arnold, 1988), the sponges (>1500 species), prawns (Gribble, 1997), cephalopods (Moltschaniwskyj & Doherty, 1994, 1995), and the fishes (e.g., Newman & Williams, 1996; Newman et al., 1997; Williams & Hatcher, 1983).

These patterns are connected with major cross-shelf changes in physical factors around the 22- to 23-m isobaths. These include changes in nutrients, turbidity, wave action at the seabed, sediment type, and sediment re-suspension rates, which manifest as a progression in the structure and function of pelagic and benthic communities (see Alongi, 1997 for review). Northward, longshore predominance of water movement is partially responsible for an abrupt change from well-mixed coastal waters overlying terrigenous silts, clays, quartz, and silica sands to clear, nutrient-poor waters overlying sedimentary deposits increasing in carbonate content seaward (Belperio & Searle, 1988). The discontinuity in biodiversity of a range of benthic communities in this gradient can sometimes be sharp, with a transition between "inshore" and "lagoonal" zones occurring in as little as 500 m (Birtles & Arnold, 1988). In other cases the transition is much more gradual (Jones & Derbyshire, 1988; Watson et al., 1990).

The largest source of modern terrigenous sediment for the GBR shelf is direct fluvial input during discrete flood events in the wet season. These pulses are most dramatic—and variable—in the dry tropics. Variability at annual and decadal scales is linked to the passage of tropical cyclones and the strength and duration of the summer monsoon caused by ENSO climate variability (Lough, 1998; Mitchell & Furnas, 1997). For example, the Burdekin River is dominant with mean annual flow of 9.272×10^6 Ml, but this statistic hides the extremes of drought and flood forcing geological, hydrological, and biological processes in the coastal fringe and reefs. The range of annual flows is 0.54×10^6 to 50.927×10^6 Ml, with a coefficient of variation of 116.7% (Wolanski, 1994).

Flood plumes enter the GBR lagoon mostly between 17 and 23°S and typically flow northward, and the residence times of dilute patches inside headlands are in the order of a few weeks. In the 1981 Burdekin River flood peak, the entire Upstart Bay was filled with freshwater and a plume of brackish water (<18 ppt) stretched 100 km northward along the coast. At this time the surface salinities over the 15- to 20-m isobaths off Bowling Green, Cleveland, and Halifax Bays were 15 to 30 ppt, and significant seawater dilution at the seabed was measured in these depths (Wolanski, 1994). The plumes can cause coral mortality on coastal fringing reefs and also travel on the surface to outer-shelf reefs (Furnas et al., 1997; Mitchell & Furnas, 1997) affecting coral metabolism and calcification rates sufficiently to cause recognisable signatures in skeletal growth bands (Isdale, 1984).

The ocean interface with these fluvial inputs can occur in a hydrodynamic shear zone in the general region of the central lagoon that may shift inshore and offshore from the 22- to 23-m isobaths, or disappear, with prevailing winds. Whilst there is no evidence that this shear zone causes cross-shelf changes in benthic community composition and diversity, its nature demonstrates important connections between physical oceanography and biology. The poleward flowing East Australian Current pushes water onto the outer shelf, southward through the reef matrix, and through major passages (such as Magnetic and Palm Passages). Under typical southeasterly wind conditions that shallow body of water trapped against the coast moves in the opposite direction, northward (Wolanski, 1994). The result is a velocity shear and a zone of low residual displacement, found by Moltschaniwskyj and Doherty (1995) in the middle of the lagoon in the central GBR (24 to 33 km offshore), and marked by gradients in temperature and salinity.

The cross-shelf location of this feature (known as a separation front or "coastal boundary layer") is predicted in models to shift seaward with increasing SE wind strength, and vice-versa (Wolanski, 1994). High secondary productivity (McKinnon & Thorrold, 1993; Thorrold & McKinnon, 1995) and high densities of juvenile and larval fish and cephalopods (Thorrold, 1992; Moltschaniwskyj & Doherty, 1995) indicate that this area is important both biologically and hydrodynamically. The juvenile and larval fishes include reef fish taxa found farther offshore as adults, as well as piscivorous larvae of various mackerels and tunas from inshore (Thorrold, 1993). These studies suggest juvenile fishes and cephalopods in this low shear zone were either aggregating there, actively or passively, or had better survivorship—or combinations of all these factors. Increases in zooplankton abundance and in copepod egg production have been measured in rapid response to both wet season flood plumes and to episodes of upwelling and cross-shelf intrusion of Coral Sea water (Thorrold & McKinnon, 1995). These data support the suggestion by Alongi (1997) that some members of the coastal and offshore zooplankton and benthic communities in the GBRWHA are "opportunistic, poised to respond quickly to these climatological and hydrographical events."

There are also a wide variety of wind-driven surface features that structure the pelagic environment of the GBR lagoon and act to attract or passively aggregate and transport pelagic stages of fish, crustaceans and cephalopods, and their prey (see Kingsford, 1990 and 1995). These include the phenomena of Ekman drift and

Langmuir cells, as well as wind-rows of drift algae (e.g., *Sargassum*) and flotsam (see Figure 1) that provide food and shelter for pre-settlement stages—or act to transport them across boundary currents toward shore (Kingsford et al., 1991). Pre-settlement stages of the tripletail (*Lobotes surinamensis*) and batfish (*Platax* spp.) adopt striking mimicry of the shape, colour, and motion of floating leaves in these slicks. A variety of large pelagic scombrids and carangids actively feed at the surface on the small fishes and crustaceans sheltering in these surface features of the GBR lagoon.

In summary we suggest that for some materials and processes, and outside the occurrence of cyclonic disturbances and flood pulses, the 22- to 23-m isobaths may represent the general "land–ocean interface" within reef and inter-reef dynamics. However, far too little is known of bentho-pelagic coupling, carbon and nitrogen cycling, and interconnections between lagoonal waters and the GBR matrix to elaborate sophisticated food web models or nutrient budgets for this tropical shelf (Alongi, 1997).

CROSS-SHELF AND INTER-OCEANIC CONNECTIVITY THROUGH FOOD CHAIN LINKS

Obvious transfer of material away from vegetated habitats occurs in the form of floating "litter"—mangrove propagules, leaves, wood and root material, and seagrass seeds, flowers, blades, and rhizomes. Early overseas studies in Florida established a paradigm that stressed the importance of mangrove forests in supporting nearshore secondary production via detrital-based food chains (e.g., Odum & Heald, 1975). Connections between saltmarsh, mangrove, and seagrass communities and those farther offshore in the GBRWHA have since been examined within the context of "outwelling"—the export of nutrients or organic detritus from fertile estuarine areas to support productivity of offshore waters (see Robertson et al., 1992; Alongi, 1997 for reviews). The amount of material exchanged is influenced not only by rate of primary and secondary production in vegetated coastal habitats, but also by physical characteristics of geomorphology, exposure to tide and wave energy, heat, light, and rainfall—to the extent that each system is unique (Alongi, 1990a, b, and c; Alongi et al., 1989). However, recent reviews (Butler & Jernakoff, 1999; Alongi, 1997) indicate few data are available on outwelling from Australian saltmarshes and seagrasses. Despite their proximity to major coastal nurseries the extent of material connectivity between mangroves and adjacent seagrass beds and saltmarshes also remains unknown in Australia (Robertson & Duke, 1987; Robertson et al., 1992).

Surprisingly, in the GBRWHA the "outwelling" of mangrove material is of limited importance in the coastal zone, since little material (relative to the enormous total tree production and standing biomass) is exported from the forests—and generally not more than a few kilometres from the mangrove estuaries (see Robertson et al., 1992; Alongi, 1997 for reviews). This carbon does have a significant impact on sedimentary nutrient cycles, but does not translate into a significant dietary subsidy for fish and prawns and other coastal macro-organisms outside the forests, despite the fact that juveniles of some penaeid prawns feed on mangrove detritus or on meiofauna that is mangrove dependent (Alongi et al., 1989). These findings have recently been supported by studies using stable isotopes to trace food chains supporting juvenile penaeid prawns, which showed the primary source of carbon depended on the location within estuaries (Loneragan et al., 1997). Seagrass and associated epiphytes were traced as most important in supporting feeding by juvenile tiger prawns (*Penaeus esculentus, P. semisulcatus*) in seagrass beds in mangrove-lined estuaries, despite the proximity to mangroves and the presence of large quantities of mangrove detritus in the seagrass beds. The considerable amount of mangrove and terrestrial carbon exported from tropical Australian estuaries during the wet season was considered to be unlikely to contribute to offshore food webs supporting adult prawns, with benthic microalgae or seagrass detritus possible sources on the coastal grounds. Furthermore, the contribution of mangrove/terrestrial sources to the food of juvenile banana prawns (*P. merguiensis*) appeared to be limited to small spatial scales, within the mangrove fringe of small creeks and mainly during the wet season (Loneragan et al., 1997; Vance et al., 1996).

Whilst "outwelling" from the coast has not been measured to be as important as widely perceived, substantial connectivity does occur through the movement of large bundles of protein (in the form of prawns, baitfish, and other organisms) across shelves from coasts to reefs. In the case of mangrove export the early Florida model of food chains (Odum & Heald, 1975) had as its base mangrove litter, thought to be flushed into mangrove waterways where microbial decomposition occurred to promote saprophytes upward to consumers of detritus, and their predators. However, later work showed that consumption and retention of litter within forests by sesarmid and ocypodid crabs has profound effects on pathways of energy and carbon flow within forests, the quantities of material available for export from the forests, and nitrogen cycling within them (see Robertson et al., 1992; Lee, 1998 for reviews).

In turn, the leaf-burying mangrove crabs provide a fundamental link between mangrove primary production and coastal food chains (Robertson & Blaber, 1992). Recruitment of larval fish into mangrove waterways peaks in the Townsville region during mid-summer (Robertson & Duke, 1990a and b) in coincidence with the outflow on ebb tides of vast numbers of crab zoeae, which are consumed by zooplanktivorous, juvenile fish (see Robertson et al., 1992). Studies in progress of adult diets of predatory estuarine fish showed a predominance of adult sesarmid and other grapsid crabs in the diet of spotted-scale sea perch (*Lutjanus johnii*), mangrove jack (Robertson et al., 1992), estuary cod (*Epinephelus coioides, E. malabaricus*), and other major angling species (M. Sheaves, personal communication). Other major outflow of invertebrate protein occurs through spawning swarms of polychaete worms at the surface of mangrove forest waterways in mid-summer, and sub-littoral swarms of the sergestid shrimp *Acetes sibogae australis* (Omundsen et al., 2000). These shrimp are visibly important to scyphozoan "box" jellyfish (*Chironex, Chiropsalmus*), manta rays (*Manta* spp.), and a variety of other predators. Other direct links within the mangrove estuaries are visible between mud crabs (*Scylla serrata*) which eat the large *Telescopium* and other gastropods (I. Knuckey, personal

signatures in wrasse otoliths to show that recruitment to an island population may often result from local retention on leeward reefs. Both studies indicate that models that overemphasise downstream dispersal of passive larvae (to "sinks") will not predict the long-term behaviour of populations, inside or outside marine reserves set up to preserve "sources."

The life histories of many major reef fish families are poorly known, but there is an increasing awareness that larval or juvenile dispersal inshore occurs to turbid, shallow waters and vegetated habitats for some scombrids, lutjanids, serranids, and lethrinids associated with reefs as adults. This is followed to a greater (e.g., mangrove jack) or lesser degree (*Lutjanus johnii*) by offshore ontogenetic migration (e.g., Newman & Williams, 1996; Newman et al., 1997) to spawning grounds amongst the reef matrix or the inter-reef megabenthos. Mangrove jack penetrate nursery areas as far upstream into freshwater as physical barriers and oxygen concentrations will allow. The immature fish then move offshore from mangrove habitats (presumably utilising inter-reef isolates and gardens en route: see Figures 1, 5, and 6) at about 45 to 48 cm length and 6+ to 8+ years of age to mature in deeper waters (Sheaves, 1995). This cross-shelf movement has been directly demonstrated by increasing numbers of tag returns from the "AusTag" Sportfish Tagging Program for both mangrove jacks and black-spot estuary cod (*Epinephelus malabaricus*) (Sawynok, 1999). Crustaceans also move offshore to reach spawning grounds—at the edge of the shelf break in the case of mud crabs (*Scylla serrata*) (Hill, 1994) and ornate rock lobster (*Panulirus ornatus*) (Moore & MacFarlane, 1984) in the GBRWHA.

Fish size generally increases with depth for red emperor *Lutjanus sebae*, and the sea-perches *L. malabaricus* and *L. erythropterus* (McPherson et al., 1992), indicating progressive offshore movement, but there are important differences in ontogeny. Juvenile *L. malabaricus* and *L. erythropterus* ≥2.5 cm long occur in large bays of the Central GBR, especially around sparse seagrass beds (Williams & Russ, 1994; Newman & Williams, 1996; Newman et al., 1997) and also inside estuaries of the far northern section (D. Donald, personal communication). They are restricted to depths <15 m with high silt and clay fractions in the Central GBR, including sea-grass beds, whereas juvenile *L. sebae* have a much wider depth range and can be found over both terrigenous and carbonate sediments in the range 15 to 62 m (Jones & Derbyshire, 1988). Red Emperor juveniles can be caught on the same inter-reef grounds over high-relief shoals and wrecks and exposed Pleistocene reef surfaces as mature adults, and there is some evidence that they may be less common than *L. malabaricus* and *L. erythropterus* in turbid waters of 5 to 15 m (A. Zavodny, personal communication; Williams & Russ, 1994).

It is also important to recognise that connection of other ecosystems with the GBRWHA occurs at between-ocean scales, in the case of migrations by humpback whales (*Megaptera novaehollandiae*) and other cetaceans, seabirds, black marlin (*Makaira indica*), and sea turtles (see Marsh et al., 1997). In the case of black marlin, mature fish congregate in the northwest Coral Sea, in the Cairns–Lizard Island region, to spawn between September and December. Their piscivorous larvae are most common within 0.25 nm of the reef crest after this spawning, presumably in coincidence with high prey abundance (P. Speare, personal communication).

A southward migration of young-of-the-year and 2-year-old fish then occurs from northern Queensland (see below) to central New South Wales in association with the progression of the East Australian Current. Tagged fish in a wide range of sizes have moved large distances (up to 7200 km in 359 days) to and from the GBRWHA. Recaptures of fish near their points of release after 1, 2, 3, or 4 years strongly suggest annual homing of at least mature parts of the population to the northwest Coral Sea (Pepperell, 1990).

Long-shore feeding and spawning migrations through various portions of the GBR lagoon have also been demonstrated for a variety of "lesser" (*Scomberomorus munroi, S. queenslandicus, S. semifasciatus*) (Begg et al., 1998) and Spanish (*S. commerson*) mackerels (McPherson, 1987). In the central section during the months of October and November the Spanish mackerel migration (from perhaps as far south as New South Wales) culminates in spawning aggregations around Rib reef and other mid-shelf reefs close to major passages (McPherson, 1997). Numerous carcharhinid sharks accompany the schools. The currents in these locations may aid larvae in dispersal to inshore feeding grounds and nurseries, and these larvae have been caught in light traps at the "coastal boundary layer" nearby (Jenkins et al., 1984 and 1985; Thorrold, 1993).

Inshore spawning migrations are also known for at least eight species of whaler (Carcharhinidae) and hammerhead (Sphyrnidae) sharks, whose adults move into shallow bays to pup in early–mid-summer. The bull shark (*Carcharhinus leucas*) pups inhabit estuaries and the freshwater reaches of suitable wet-tropics rivers. The bays are communal nursery areas for these sharks, which have similar diets comprising mainly fast-growing, planktivorous engraulid and clupeid baitfish. There is a seasonal coincidence between highest numbers of shark juveniles and highest prey abundance (Simpfendorfer & Milward, 1993). This temporal coincidence of juvenile predators and recruitment pulses of prey resources occurs also for the lesser and spanish mackerels (see Jenkins et al., 1984 and 1985).

A CASE STUDY OF BAITFISH–PREDATOR LINKS

A prime example of the temporal, spatial, and ontogenetic scales we have sought to portray occurs annually in striking circumstances between the 20- to 40-m isobaths offshore from mangrove-lined bays in the Cairns, Dunk Island, and Bowling Green Bay regions. Each winter, aggregations of clupeid, carangid, and scombrid baitfish and teleost, elasmobranch, avian, and cetacean predators occur in "billfish grounds" in the middle of the GBR lagoon (Williams, 1990). These aggregations represent food chain connectivity across-shelf in the movement of baitfish (Williams & Cappo, 1990), and along-shore, in the southward movement of juvenile black marlin (Pepperell, 1990; Speare, 1994) and the northward movement of maturing Spanish mackerel (McPherson, 1987 and 1997) and spotted mackerel (Begg et al., 1998).

Off Cape Bowling Green (see Figure 8), the baitfish species school in large surface aggregations and are hunted from below by schools of young-of-the-year black marlin, pods of adult sailfish (*Istiophorus platypterus*) and dolphins (*Tursiops*