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Graph theoretic topology of the Great but small Barrier Reef world

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Abstract The transport of larvae between coral reefs is critical to the functioning of Australia's Great Barrier Reef (GBR) because it determines recruitment rates and genetic exchange. One way of modelling the transport of larvae from one reef to another is to use information about currents. However the connectivity relationships of the entire system have not been fully examined. Graph theory provides a framework for the representation and analysis of connections via larval transport. In the past, the geometric arrangement (topology) of biological systems, such as food webs and neural networks, has revealed a common set of characteristics known as the 'small world' property. We use graph theory to examine and describe the topology and connectivity of a species living in 321 reefs in the central section of the GBR over 32 years. This section of the GBR can be described by a directional weighted graph, and we discovered that it exhibits scale-free small-world characteristics. The conclusion that the GBR is a small-world network for biological organisms is robust to variation in both the life history of the species modelled and yearly variation in hydrodynamics. The GBR is the first reported mesoscale biological small-world network.

Keywords Small world · Coral reefs · Scale free · Graph theory · Metapopulation

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Introduction

The transport of larvae between coral reefs is critical to their function because it determines recruitment rates and genetic exchange (Veron 2002; van Oppen and Gates 2006). Dispersal processes for marine organisms are diverse (Ninio and Meekan 2002; Mora et al. 2003) but two main types can be identified: the brooders and broadcasters. Each of these strategies affects the fraction of larvae from one reef that arrives at another. For broadcasters in particular, the pre-competent larvae will drift in a relatively passive manner with the currents (Ayre and Hughes 2000). Strong currents can transport larvae over long distances for several weeks while they remain pre-competent (Ayre and Hughes 2000). Both local and distant populations can be linked by this transport of larvae.

The processes that shape the diversity of Australia's Great Barrier Reef (GBR) are complex and dependent on a range of biophysical factors (Hughes et al. 1999; Sale 1999; van Woesik 2000; Brinkman et al. 2001; Harriott and Banks 2002), including water currents that transport larvae and warm water (Mora et al. 2003). The oceanic flow, called the Eastern Australian Current, interacts with the tidal cycles and wind conditions to provide transport mechanisms (Brinkman et al. 2001; James et al. 2002) for the exchange of larvae between reefs throughout the central and southern GBR (Ayre and Hughes 2000; Harriott and Banks 2002). While there is general acceptance of the importance of these processes, their implications for the function and management of the GBR has not been fully examined.

While many studies describe the transport of larvae from one reef to another (Swearer et al. 1999; James et al. 2002; Siegel et al. 2003; Nishikawa and Sakai 2005), the effect on the entire system has not been fully examined (Mumby

1999). Over an extended period, larval transport linkages create a recruitment network, the structure of which determines the nature of interactions between distant reefs. Matrices describing a single recruitment event have been calculated (James et al. 2002; Bode et al. 2006). One way of assessing the role each reef has within the entire network is to use graph theory (Franc 2004; Proulx et al. 2005).

Graph theory models of disparate systems, like the World Wide Web, metabolic pathways, the neural network of a worm, electronic circuit design and the professional relationships of film actors, have found networks that are highly clustered and well connected (Hayes 2000; Ferrer et al. 2001; Wagner and Fell 2001). Biological systems, from metabolic pathways (Jeong et al. 2000) to lake trophic structures (Montoya and Sole 2002) and the neural networks of a worm, all show a relatively new pattern called a 'small world' (Watts and Strogatz 1998). This pattern is named after the universal exclamation of 'what a small world!' when strangers appear to be closely associated by mutual connections (Watts and Strogatz 1998). First described in sociometry research (Milgram 1967; Travers and Milgram 1969), small worlds describe how community formation can facilitate the effective interaction of distant individuals across an entire population where there are only interactions between small groups of neighbours (Radicchi et al. 2004).

Graph theory has been applied to ecological research previously but with a focus on measuring simple landscape indices such as dispersal pathway length (van Langevelde et al. 1998; Bunn et al. 2000; Urban and Keitt 2001). These landscape connectivity graphs that record the movement of wildlife are relatively simple due to the difficulty in recording the movements of individual animals. While these graphs form a foundation for the use of graph theory in ecology, they lack the size and intricate structure for complex network analysis, especially when compared with the forest songbird habitat network of Minor and Urban (2008).

In this study, we use graph theory to examine and describe the network topology of species inhabiting 321 reefs in the central section of the GBR (Fig. 1) based on 32 years of connectivity matrices generated by James et al. (2002). In particular, we ask three questions: (1) Is the GBR a scale-free small-world network for marine organisms? (2) Do variations in the dispersal model parameters (duration of the precompetent period, the size of the settlement zone, predation and when larvae are released) influence the pattern? (3) How influential is the connection strength on the network metrics?

Graph theory, small worlds and scale-free distributions

Graph theory is a branch of mathematics that describes the statistical nature of simple (Harary 1969; Gross and Yellen

1999) and complex (Dorogovtsev and Mendes 2002; Proulx et al. 2005; Steuer and Lopez 2008) static networks. A graph $G(V,E)$ can be defined as a finite set of vertices V, connected by edges E (Fig. 2). Geometric theorems of the properties of simple graphs dominated the use of graph theory until the advent of fast computers. Large graphs were modelled as randomly assembled graphs or as regular lattices (Albert and Barabasi 2002).

The degree (k_i) of a vertex i defines the number of connecting edges and hence the number of neighbouring vertices (Fig. 2). All vertices in a regular lattice share a common degree, $<k>$, and this configuration (often displayed as a grid of equally sized cells) is commonly used as the basis for neighbourhood interaction models (Bjornstad et al. 1999; Vuilleumier and Metzger 2006). In a random graph, the degree of all the vertices has a Poisson distribution and is characterised by a modal hump at the mean degree (Proulx et al. 2005). The average degree for all the vertices in a graph is denoted as $<k>$.

The clustering coefficient, as defined by Montoya and Sole (2002), is the sum of the number of triangular linkages $\vartheta_i (i \in V_1, ..., V_n)$ within the set of neighbours (Fig. 3) for a selected vertex divided by the maximum possible neighbour linkages where n is the number of vertices in the network. For a unidirectional network, there are potentially $k(k-1)/2$ triangular linkages. The clustering coefficient is thus defined as:

$$CI = \frac{2}{n} \sum_{i=1}^{n} \vartheta_i / (k_i(k_i - 1)). \qquad (1)$$

The graphs modelling the GBR are directional weighted graphs. For a directional network, there are potentially twice as many, $k(k-1)$, triangular linkages and so the clustering coefficient is redefined from Eq. 1 as:

$$CI = \frac{1}{n} \sum_{i=1}^{n} \vartheta_i / (k_i(k_i - 1)). \qquad (2)$$

The average minimum path length L is the average number of edges in the shortest path $L_{\text{Min}}(i, j)$ between all pairs $V(i, j)$ in a graph averaged over $n(n - 1)/2$ vertices (Montoya and Sole 2002)

$$L = \frac{2}{n(n-1)} \sum_{i=1}^{n} \sum_{j=1}^{n} L_{\text{Min}}(i,j). \qquad (3)$$

Calculation of the average minimum path length encompassed the directional structure of the network by forcing the path tracing routine to travel in the direction of lines. The assumption in Eq. 3 that $L_{i,j}=L_{j,i}$ is relaxed in an asymmetric graph, and thus, the summa-
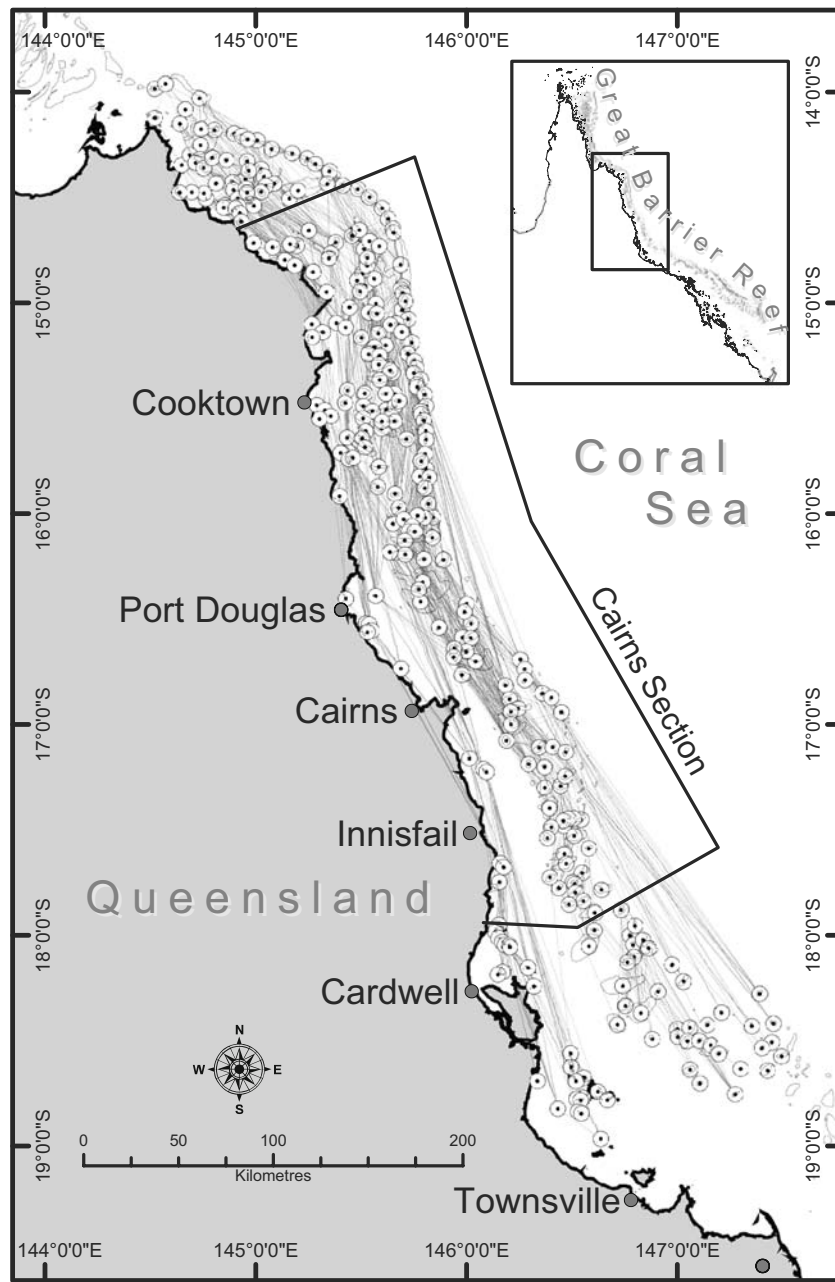
Fig. 1 Graph of 1998 connectivity with hydrodynamic parameters of release by new moon, 1 km pick up zone, 1 week pre-competent period, 3 weeks competent period and no predation. The edges displayed are only those with weight greater than 0.02

Fig. 2 A simple graph containing five vertices and seven edges. Four of the vertices have a degree of 3; one has a degree of 2
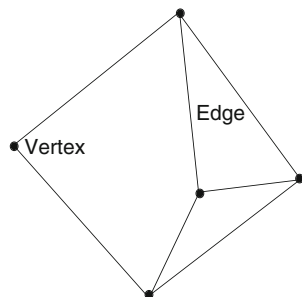
Fig. 3 Neighbourhood triangle (*dashed lines*) forms the basis of the clustering coefficient. Average minimum path length highlights the number of steps (*labelled*) to reach the target vertex
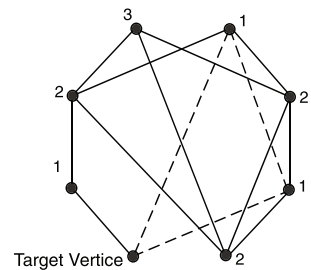
tion of path lengths is averaged over possible between-vertex connections, $n(n-1)$:

$$L = \frac{1}{n(n-1)} \sum_{i=1}^{n} \sum_{j=1}^{n} L_{\text{Min}}(i,j). \quad (4)$$

As a consequence of measuring the paths through the network, three more metrics can be usefully derived: diameter, closeness and betweenness (Freeman 1978). The diameter, D, is the *longest* minimum path length that exists between any vertices in a network. The closeness centrality measure, CC_i, is the sum of the minimum path lengths connecting a vertex i to all other vertices j ($i, j \in V_1,...,V_n$). The betweenness centrality measure, BC_k, is the proportion of minimum paths connecting vertices i and j that pass through vertex k ($i, j, k \in V_1,...,V_n$). The centrality measures relate to the isolation (low CC), contagion (high CC) and 'stepping stone' (high BC) landscape ecology concepts (Gustafson 1998).

Graphs that have a high level of clustering and short path lengths compared with random or regular lattices are known as small-world graphs (Watts and Strogatz 1998). However, there is no explicit definition of the properties of small-world graphs (Schnettler 2009). Small-world topology increases the connectivity of vertices, effectively making it smaller, in terms of interactions, than a random or regular one. Clusters connected by longer links enable any point in the network to be located a small number of steps from any other point, and this forms the basis of Stanley Milgram's six degrees of separation for the network describing human social interactions (Barabasi 2002).

An additional characteristic of some small-world networks in the real world is that the number of vertices with k connections can be described by a power-law $P(k) \sim k^{-\gamma}$ where γ is a constant (Barabasi et al. 2000). This property, referred to as a scale-free degree distribution, defines a graph where the majority of vertices are weakly connected and a small, but significant, number are very strongly connected (Albert et al. 2000). In contrast in a random graph, the number of vertices, n, with degree, k, shows a Poisson distribution where few, if any, vertices are very strongly connected. However Li et al. (2005) present a convincing argument that the power law used in many publications does not represent a scale-free network consistently, and instead, they suggest the use of the size-rank measure: $R(k) = cY_k^{-\gamma}$, where $R(k)$ is the rank of the degree y_k subject to y_k being from a finite sequence such that $y_1 \geq y_2 \geq .... \geq y_n$ and c is a fixed constant and γ is a scaling index.

While the number of connections reveals many of the topological structures, the strength of each connection can be used to describe the exchanges between the vertices. In the case where the strength of connection between two vertices is known, the value of the edge weight, w_{ij}, describes the intensity of interaction occurring between vertex i to vertex j. The inbound and outgoing strength indices for vertex i are defined (Barrat et al. 2004; Newman 2004) as:

$$s_i^{IN} = \sum_{j \in v(i), j \in E_{ji}} w_{ji}, \quad s_i^{OUT} = \sum_{j \in v(i), j \in E_{ij}} w_{ij} \quad (5)$$

where $v(i)$ is the set of neighbours of vertex i, E_{ji} is the set of edges having the inbound direction to vertex i, and E_{ij} is the complementary set of edges having an outbound origin from vertex i. The average in- and outbound strengths for the entire graph are:

$$S^{\text{in}} = \frac{1}{n} \sum_{i=1}^{n} s_i^{\text{IN}} \text{ and } S^{out} = \frac{1}{n} \sum_{i=1}^{n} s_i^{\text{OUT}}. \quad (6)$$

Empirical studies of complex networks show them to be sparsely connected, tightly clustered and with a relatively small diameter (Hayes 2000), which can be described by the respective indices of degree distribution, cluster coefficient and average minimum path length (Montoya and Sole 2002). Having explained the necessary graph theory, we now describe the methodology used to create and analyse a large larval transport network for a section of the GBR.

Methods

In this section, we will outline how the larval transport network in the marine environment was constructed and analysed. For many marine organisms, the mechanism of dispersal is limited to the broadcasting of relatively passive larvae into highly dynamic water bodies (Barber et al. 2000; Shanks et al. 2003). Due to the difficulties in measuring the larval passages, connectivity research is heavily reliant on hydrodynamic simulations. Our study used connectivity matrices generated by James et al. (2002) that simulate the release of larvae from 321 reefs into a Lagrangian hydrodynamic model of the Cairns section of the GBR (Fig. 1). These matrices estimate the number of simulated fish larvae that manage to survive from the spawning reef to the settlement reef. The spawning reef can also be the settlement reef (self-seeding) but these results are not used in the graph structure since the primary aim is to examine inter-reef connections. The strength of the pairwise connections is a function of the size and shape of the donor and recipient reefs since we assume that larvae are spawned with uniform density along the reef edge. Allowing for variation of factors such as mortality rates, release timing, distance of attachment, pre-competent and competent periods, the larvae are moved around in two dimensional spaces according to currents that are driven by wind and tidal forces. The simulations extend over the period from 1967 to 1998 (Bode et al. 2006) and focus only on the

summer months when dispersal is concentrated (James et al. 2002). We consider the model to represent all larvae that have the dispersal properties with the parameters used in the James et al. (2002) model, and hence, this can also include coral larvae. Due to lengthy processing time required to run the hydrodynamic model, the capacity to conduct sensitivity tests on these dispersal parameters is limited.

We transformed the James et al. (2002) connectivity matrices into graphs using tools created in both R statistics (especially utilising packages 'igraph' (Csardi and Nepusz 2006) and 'sna' (Butts 2007)) and within an ArcGIS 9.3 (Environmental Systems Research Institute, Redlands, USA) environment. Where the strength of connection is greater than zero, a line is constructed between points representing reefs. The line has the attributes of connection strength, distance and direction of flow. The reef centroids have the spatial attributes of area, perimeter and location.

We addressed the initial questions in the following manner.

1. Is the GBR a scale-free small-world network? The values of average minimum path length (L), average degree ($<k>$), connection strength (S), diameter (D), edge number (E) and cluster index (CI) were analysed for the years 1967 to 1998 and compared with other networks of various topologies. The constructed networks, used for comparison and described in Table 1, contained the same number of vertices and, where possible, the same average degree. To examine the role of individual reefs in maintaining high larval flow through the network over time, the closeness and betweenness centrality metrics were used.

2. How robust is our small-world emergent property to the life history characteristic of species? The release timing, distance of attachment, pre-competent and competent periods are altered using the hydrodynamics of 1998 to examine the changes in average minimum path length (L), connection strength (S) and cluster index (CI).

3. How influential is the connection strength on the graph topology? Using the 1998 graph, we removed the connections in 15 equal steps based on three different strategies; strongest links removed first, weakest links removed first and randomly selected links removed. We considered the impact on: average minimum path length (L), edge number (E) and cluster index (CI). We also compare the Euclidian distance and the weight derived from the hydrodynamic model for each edge.

Results

Is the GBR a small-world network? The average minimum path lengths, L, (Fig. 4), for the GBR from 1967 to 1998 (with parameters of day release, 1 km pickup zone, 1 week pre-competence, 3 weeks competent and no predation (James et al. 2002)), are in the range 2.2 to 3.9 links, and the average cluster coefficient, CI, is in the range of 0.26 to 0.31. The average degree $<k>$ ranges from 128 to 67 ($\langle k \rangle = 105.93, \sigma_k = 14.04$), while the edge count E ranges from 20,554 to 10,860 ($\overline{E} = 16,950.2$, $\sigma_E = 2,247.2$). These GBR hydrodynamic networks are comparable to the constructed small-world networks (Table 1) of Watts and Strogatz (1998) and the Forest Fire Network (Leskovec et al. 2007) and more clustered than the classic Barabasi–Albert (Barabasi and Albert 1999) and Erdos–Renyi (Erdos and Renyi 1959) networks (Fig. 5). The 1998 network was rewired randomly (0.5 probability) while preserving the original graph's degree distribution, and this had the effect of reducing the clustering coefficient. Other models included in Fig. 5 were the Tree model, 2D lattice (or planar graph) and Star graph (every single vertex is connected to the centre vertex only). The centrality measures showed a large diameter network

Table 1 Alternative networks for comparison

| Model name	Description	Source
Watts-Strogatz network	Firstly, a regular lattice is created, then the edges are rewired uniformly with a specified probability	Watts and Strogatz 1998
Forest Fire network	This network model resembles how a forest fire spreads by igniting trees close by. Vertices are added sequentially, and edges are created with respect to the neighbouring configuration	Leskovec et al. 2007
Barabasi–Albert network	In this model, one vertex is added in each time step, and edges are then created to link existing vertices with a scale-free probability, $P(k) \sim k^{-\gamma}$	Barabasi and Albert 1999
Erdos–Renyi network	This simple network creates the complete set of vertices and then adds edges chosen uniformly randomly from the set of all possible edges	Erdos and Renyi 1959
Tree network	This model is based on a regular tree with 2 edges connecting the 'child' neighbours	Csardi and Nepusz 2006
2D lattice	A lattice of two dimensions is composed of a set of four vertices joined in a square, which is then replicated for the specified size of the network	Csardi and Nepusz 2006
Star graph	In this simple network, every single vertex is connected to the centre vertex only	Csardi and Nepusz 2006
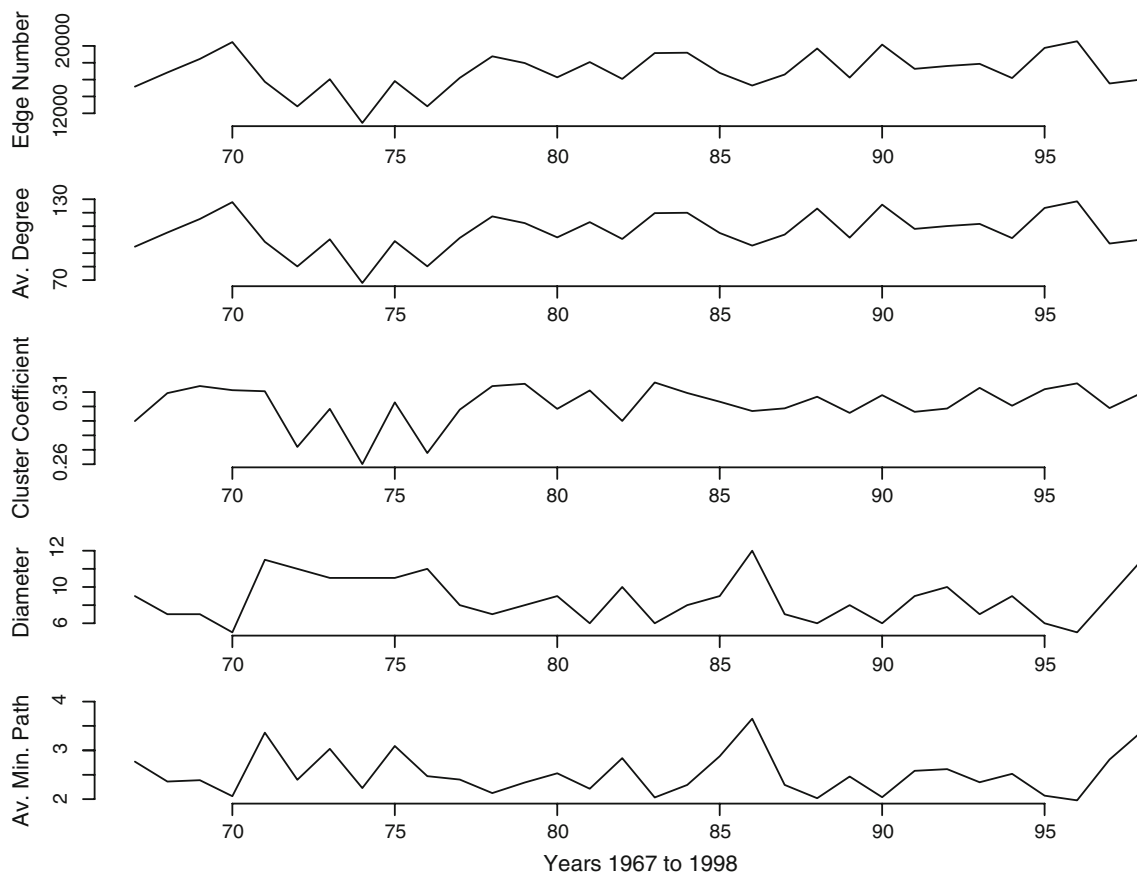
Fig. 4 The graph shows the graph theory indices for the Cairns section of the GBR for the years 1967 to 1998, assuming the hydrodynamic model parameters of new moon release, 1 km sensory settlement zone, 1 week pre-competence, 3 weeks competent and no predation. Metrics used are edge number (*E*), vertex number (*N*), diameter (*D*) average minimum path length (*L*), average cluster coefficient (*CI*), average strength (*S*) and average degree (<*k*>). From 1967 to 1998, the graphs consistently show small-world topologies

$(\overline{D} = 8.68, \sigma_D = 2.45, 5 \leq D \leq 14)$ with an exponential distribution of the betweenness measure $(\overline{BC} = 17,300, \sigma_{BC} = 25,176, 45.26 \leq BC \leq 178,125)$, which highlighted that a small number of reefs were acting as stepping stones. The closeness measure $(\overline{CC} = 16.99, \sigma_{CC} = 1.90, 11.32 \leq CC \leq 21.61)$ showed a normal distribution

that describes that some reefs are isolated while others are strongly connected. For each measure of high CC, low CC and high BC, the reefs with highest rank were identified and examined through the 32 years (Fig. 6). The plots show that these reefs were consistent for the respective centrality measure through time.

Fig. 5 Comparison with alternative models for the key small-world metrics of average minimum path length (*L*) and cluster coefficient (*CI*). The lower right area of the graph is considered to demonstrate small-world properties. The alternative models are described in Table 1
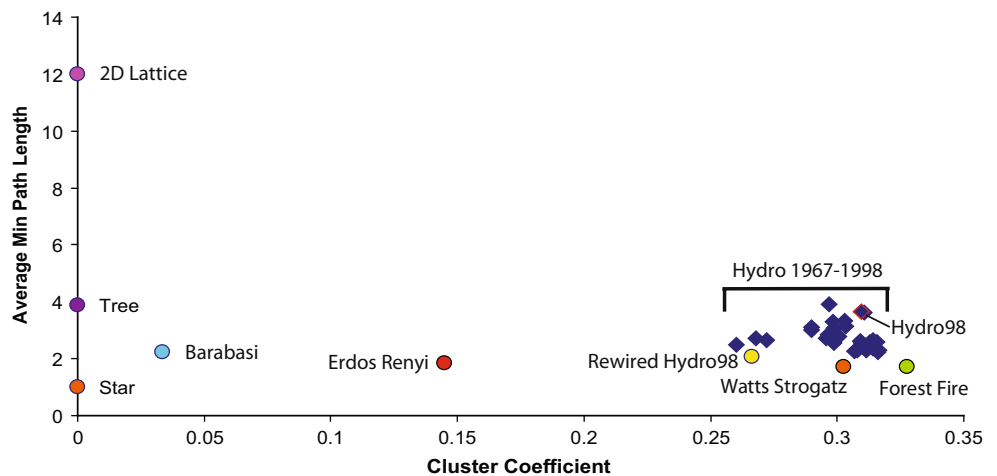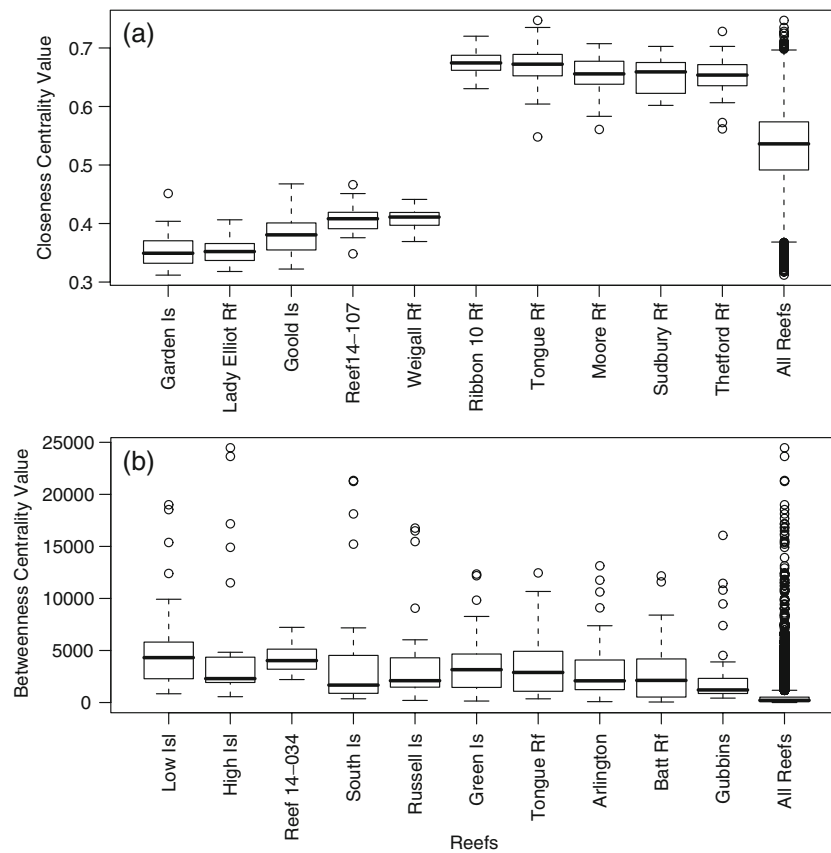
Fig. 6 Box plots of the centrality metrics for the highest ranking reefs compared with all the reefs, highlighting the individual reef consistency through the 32 years of model runs. The closeness centrality (**a**) shows the five reefs with highest and lowest values indicating the contagion and isolated reefs. The betweenness centrality (**b**) shows the top 10 reefs indicating the stepping stone or cut node reefs

The degree distribution was not found to be scale free (based on both degree frequency and size-rank metrics) for all years. This lack of scale-free degree distribution is similar to other biological networks such as the *Caenorhabditis elegans* neural network and the polymer chain model reported by Amaral et al. (2000).

Is the GBR a small-world network for the larval dispersal characteristics of different species? Varying the larval dispersal parameters showed that the average minimum path lengths, L, for the GBR from the 1998 network are in the range 2.69 to 4.31 links, and the cluster coefficient, CI, is in the range of 0.21 to 0.34 (Fig. 7). These ranges are comparable to the small-world networks shown in Fig. 5. The life history characteristics influenced the topology. Larvae released at dusk within 3 days of the new moon created networks with less clustering compared with those networks with larvae released daily during the high tide. Other life history characteristics did not influence the network consistently to the same extent; however, the average minimum path length was reduced when the competent period was shortened from 3 to 2 weeks. One particular configuration consisting of new moon release,

1 km pickup zone, 2 weeks pre-competence, 3 weeks competent and no predation produced a network with minimal average path length of $L=2.69$. This small network with a diameter of 9 became the largest network (diameter= 15, $L=4.31$) with a simple change in the competency period to 2 weeks. Altering the predation intensity did not change the small-world properties but did alter the in- and outbound *average* connection strength, S, substantially from 0.64 to 0.03.

Despite the large range in the number of edges, from 4,053 to 25,319 (mean=12,222, σ_E=5,884.23), the average minimum path lengths and the cluster coefficient showed a narrow distribution ($2.69 < L < 4.31$, $\sigma_L = 0.37$, $0.21 < CI < 0.34$, $\sigma_{CI} = 0.041$) across the parameter range. Hence, we conclude that the GBR larval dispersal network, as modelled by James et al. (2002), is a small-world network for most species.

Our third question asks how influential the strength of the connections on the graph topology is. First, let us consider the distribution of out- and inbound strength values. The inbound connection weights for the 1994 graph shows a scale-free distribution (Fig. 8), which highlights
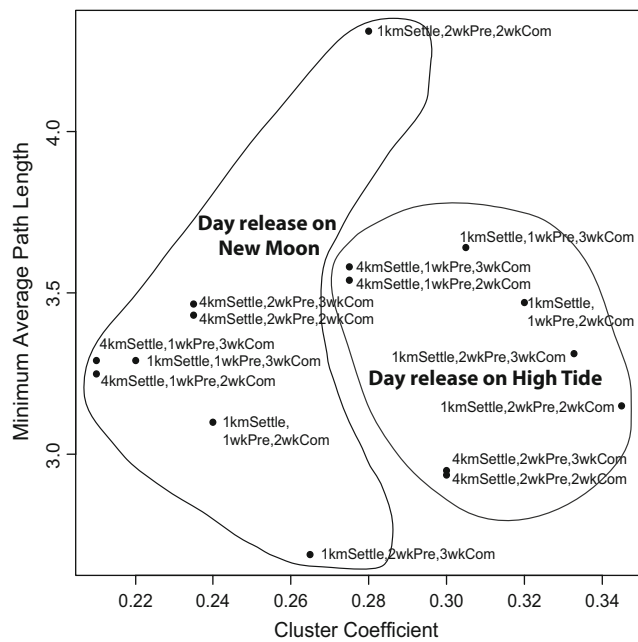
Fig. 7 A comparison of changes in the small-world metrics of average minimum path length (*L*) and cluster coefficient (CI) for reefs connected by different assumptions about hydrodynamics and species ecology. The various 1998 networks are grouped according to day release on high tide/day release on dusk with new moon and labelled with sensory settlement zone of 1 or 4 km (*1kmSettle*, *4kmSettle*), precompetent period of 1 or 2 weeks (*1wkPre*, *2wkPre*) and competent period of 3 or 2 weeks (*3wkCom*, *2wkCom*)

the sensitivity of the graph to changes in strength thresholds. The inbound strength distribution (Fig. 8a) can be described as $R(k) = cY_k^{-\gamma}$, where $Y_k = s_k$ and $\gamma = 1.38$ for the 1994 graph. The distribution of the strength values $(s_i^{\mathrm{IN}}, s_i^{\mathrm{OUT}})$ shows that a significant number of reefs have a high inbound strength, indicating that these reefs were acting as strong sinks of larvae. The inbound distribution pattern did vary between the years but the majority were described as scale free. We acknowledge that the size of a reef in the James et al. (2002) model will partially determine the larval numbers released and so influence the source capacity of each reef. As a consequence, the

outbound strength distribution across all years did not exhibit scale-free trends and were similar to the 1994 network shown in Fig. 8b.

Edges (connections) in the 1998 graph were removed based on a changing weight threshold using three different strategies (strongest, weakest and randomly removed), and the edge number, average minimum path length (*L*) and cluster coefficient (CI) were recorded (Fig. 9). The weight threshold was decreased from the maximum weight value, for the strongest removal first strategy, in 15 equal increments. Similarly, for the weakest removal first strategy, the threshold was increased from the minimum weight value. The random removal strategy selected 1,011 edges each step and deleted them. The strategy of removing the strongest edges first shows that until the 13th step, where the weight threshold was equal to 0.14, only 178 edges were removed, reflecting that the 98% of edges had a weight less than 0.14 (min=1.915e−06, mean=0.002, max =0.608). This trend is also observed in the cluster coefficient (CI) and the average minimum path length (*L*), indicating that the small world character is robust for large reductions in the maximum weight values. The second strategy of removing the weakest edges initially shows a rapid reduction in edge number and subsequent changes in the small world properties. The cluster coefficient (CI) reduced rapidly to zero at step 6, highlighting that small reductions in the minimum edge weight elicit large changes on community structure. Weaker edges tend to be longer (measured by Euclidean distance, Fig. 10), and consequently, they act to bind the network together. Their removal leaves a fragmented network sparsely connected with strong edges that have short Euclidean lengths. The average minimum path length was less affected and initially rose, while edges with generally longer Euclidean lengths (Fig. 10) were removed. By step 6, the network had fractured into isolated communities with a diameter of one. The random removal strategy shows only small changes in the average minimum path length (*L*) until finally the network consists of isolated pairs of connected reefs. The
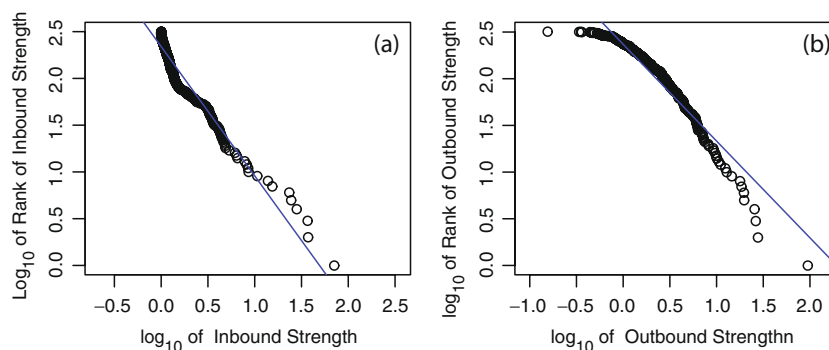
Fig. 8 Size-rank distributions of connection strength, *s* (Eq. 5), for the 1994 graph, **a** in- and **b** outbound showing the scale-free nature of the inbound strength distribution
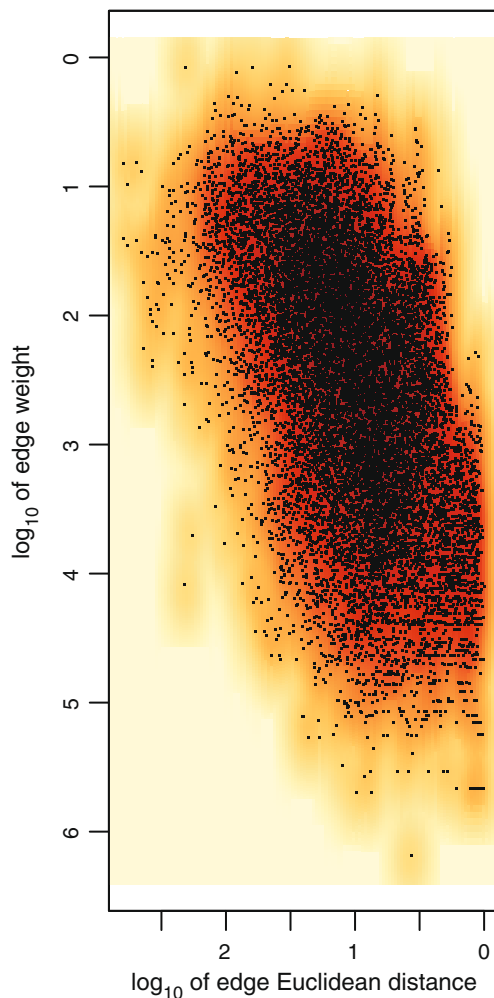
Fig. 9 Changes in the graph theory metrics, *L*, CI and *E*, for the reefs in 1998 when edges are removed based on a changing weight threshold. The three removal strategies are strongest edges removed first (*red diamonds*), weakest edges removed first (*blue squares*) and random removal of 1,011 edges per step (*green triangles*). Graph **a** shows the weight threshold used to select the edges for deletion; **b** shows the edges remaining after each step; **c** shows the changes in the average minimum path length (*L*), while **d** outlines the changes in the cluster coefficient (CI)
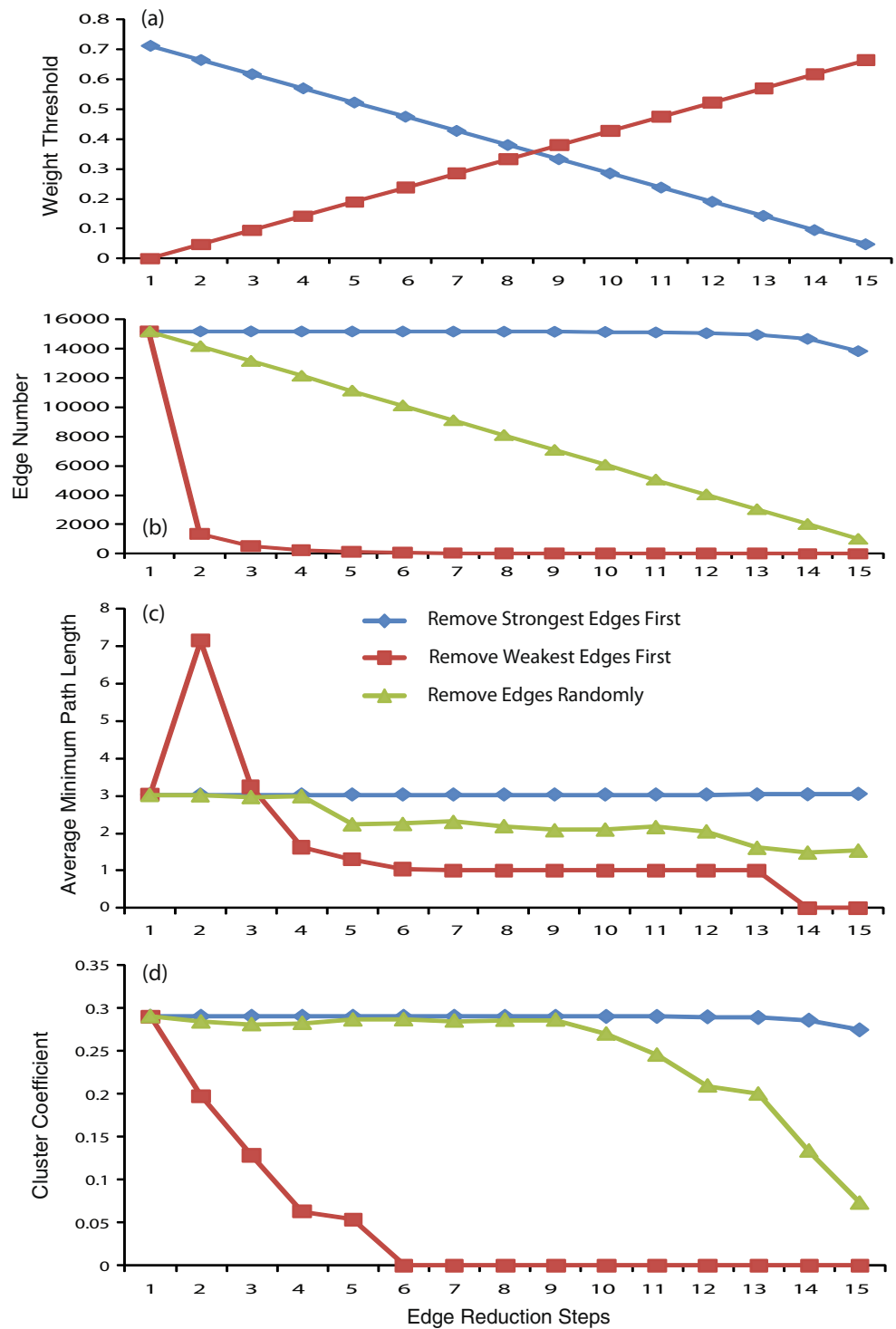
cluster coefficient (CI) did not change until approximately half the edges were removed (7,078 edges remaining from 15,167 total edges).

Next, we consider how robust the small-world network property is given changes in the edge length. The longer edges were removed (444, 333, 222, 111, 55 and 27 km) but this did not alter the topology of the graph (Fig. 11) until all the links were less than 55 km long. At this

distance, the topology of the graph altered rapidly with the average degree, $<k>$, and strength index, *S*, decreasing. At 55 km, the average minimum path length (*L*) increased as edges that connected widely separated network sections were removed from the network. However, the average minimum path length (*L*) decreased as the maximum Euclidean length was reduced to 27 km. In this case, only the smaller more consolidated network remained ($V=258$),

Fig. 10 Smooth scatter plot of all 15,167 edges for the 1998 graph showing their Euclidian distance and the weight derived from the hydrodynamic model. The strongly weighted edges tend to be shorter in Euclidean length compared to the more numerous weaker edges

network are similar to other published small-world networks of biological systems. The average minimum path length of approximately $L=3$ links with an average maximum diameter of $D=9$ links (mean arc length≈ 90 km) distributed over 600 km of reef matrix shows that the reefs are well connected relative to other sorts of graph. For example, a random network connecting the 321 reefs with the same number of connections ($D=7$, $L=2.23$) would have links with a longer average Euclidean distance, while a planar or nearest neighbour network where only the neighbouring reefs are connected ($D=34$, $L=12$) would have links with significantly shorter average Euclidean distances. The high value for the clustering index within the reef system indicates that a substantial proportion of inter-reef larvae settle on neighbouring local reefs with a smaller number travelling longer distances between clusters. This pattern is supported by the experimental evidence using particle dispersal around One Tree Island by Kingsford et al. (2002). This experiment highlighted that the majority of particles remained close to the donor reef despite the tidal influences, while a small number were swept away to more distant locations. The volume of larvae circulating in such a system need not be immense to strongly influence colonisation patterns (Ayre and Hughes 2000; Andrefouet et al. 2002; Mumby 2006; Treml et al. 2008). The role of each reef within the network, in terms of influencing larval flow, can be assessed using the centrality metrics. The results for the betweenness and closeness values (which is primarily a function of their geographic location, size and shape) show that the reefs play a consistent role through time. Conservation measures should bias protection towards these consistently important reefs.

We found that the GBR remained a well-connected small world when the life history properties of the species being
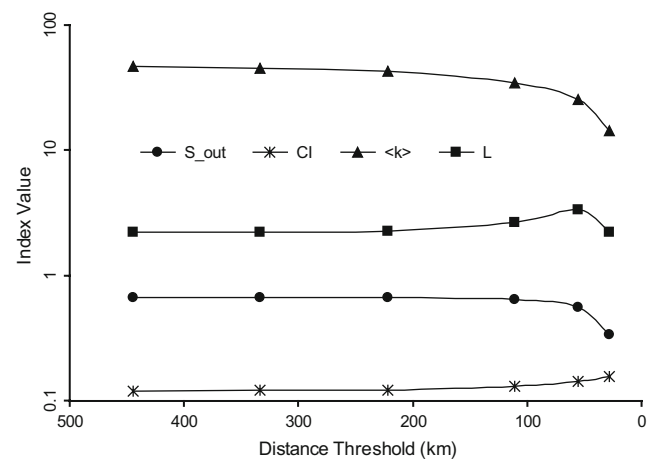
and subsequent edge length reduction resulted in fragmentation of the network. The cluster coefficient (CI), which measures the ratio of triangular linkages against the maximum possible, increased as the clusters joined by short lengths remained. The GBR remained a small-world network despite the removal of edges with lengths longer than 55 km but disintegrated into isolated clusters when the lengths were limited to less than 27 km.

Discussion

The Great Barrier Reef exhibits small-world patterns in the years 1967 to 1998 across a range of larval dispersal properties using the connectivity matrices generated by James et al. (2002). This is the first mesoscale ecological small-world network reported, and the properties of the

Fig. 11 Changes in the 1998 graph for the indices of L, S (outbound), CI and $<k>$ when the edges are incrementally removed based on their Euclidean length

modelled were varied substantially. Despite altering the mortality rates, release timing, distance of attachment and pre-competent and competent periods, the changes in average minimum path length and cluster coefficient (Fig. 7) remained within the range of other published small worlds and those artificially generated (Fig. 5). This implies that the small-world structure is the most likely structure for marine species found in the GBR marine environment notwithstanding that this network model ignores other migration processes such as adult movement that are part of the complete life cycle of marine organisms.

The GBR does not exhibit scale-free distributions of the number of connections; however, the distribution of reefs with respect to the number of larvae settling or migrating to another reef (strength of inbound connection) can be described as scale free (Fig. 8). The implications of this pattern are that the reefs in this system did not have a disproportionate number of connections, but that a substantial number of reefs were strongly connected. In contrast, weighted networks such as the world airline network and scientific authorship (Barrat et al. 2004) exhibited heavy-tailed distributions for weight. The weight of a connection in these networks will be determined by the state of the adjoining nodes (i.e. reef health and airport weather) and so understanding the impact that the state will have on the network topology and function will be essential in understanding the dynamics of the system.

Disturbances to the GBR in the form of cyclones, El Niño events and climate change are likely to impact on the way reefs are connected by larvae (Harriott and Banks 2002). The edge weight of the network, created by the hydrodynamic model, is determined by a range of complex interactions between reef topography, population fecundity, water currents and neighbourhood configuration. Within ecological time frames, only the currents and fecundity are likely to be extensively disturbed (such as El Niño events influencing the East Australian Current), and this will impact on the connection strength. The removal of weaker or stronger edges from the network (Fig. 9) reveals that the small-world character is robust when the stronger edges are diminished but the removal of the weaker edges rapidly resulted in a fragmented sparsely connected network. The more numerous weaker edges act to bind the network across the GBR, and this supports the hypothesis by Ayre and Hughes (2000) that infrequent and weak long distance dispersal is contributing to community structure across the GBR. There are strong larval connections between reefs located in relatively close proximity (Fig. 10), and field studies highlight the high levels of similarity of neighbouring populations (van Oppen et al. 2008). Random removal of dispersal edges does not alter the small world properties until only a small percentage of edges are remaining. These results imply that the GBR

small-world character is robust against random disturbance but any disturbance that results in a regional reduction in the capacity of the larvae to successfully migrate long distances will effectively and rapidly increase the GBR network size (specifically the diameter). Recovery from large scale disturbances, through external recruitment, will then be diminished.

When dispersal distances were limited to less than 27 km, the reef network broke into isolated clusters (Fig. 11), rather than a small-world pattern. Until field experiments resolve the issue of dispersal curves and self-seeding proportions for a wide range of fish and coral species (Jones et al. 1999), the small-world pattern will remain speculative. In particular, the accurate parameterisation of dispersing larvae behaviour is required for the proper use of the hydrodynamic model in predicting larval dispersal (Kingsford et al. 2002) and hence the network structure.

Numerous authors have expressed the need to include information about connectivity in planning for and managing coral reef systems (Garcia-Charton and Perez-Ruzafa 1999; Jones et al. 2005; Mumby 2006; Minor and Urban 2008). With some justification, cross shelf and latitudinal gradients dominate the ecological classification of the GBR (for example Fabricius and De'ath 2001). These classifications do not attempt to include metapopulation processes such as the dispersal of larvae, yet biodiversity protection instruments such as the marine protected areas rely on preserving these processes (Possingham et al. 2005). Graph theory provides the capability to identify how individual reefs are contributing to community structures. Prioritising reefs based on the functional role within a larval network could assist with the design of conservation reserves (Garcia-Charton and Perez-Ruzafa 1999). Maintaining the network as a strongly connected system across a diverse geographic space (inshore to outer shelf) rather than as a series of isolated communities will require the identification and protection of reefs essential to enhancing larval flow. This includes key isolated and highly connected reefs as well as stepping stone reefs such as Low Island Reef (Fig. 6).

If the GBR is a small-world network, how does this alter our perspective on the reef metapopulation? Is each reef functioning as an isolated community (i.e. Jones et al. 2005) with occasional larval exchange (i.e. Ayre and Hughes 2000)? Isolation occurs at different scales, and the hierarchical nature of small worlds describes how clusters exist within clusters and indeed some networks maybe fractal in nature (Song et al. 2005). For example, the Palm Passage (Fig. 12) provides a barrier to larval transport and effectively isolates the southern cluster from larval recruitment (Bode et al. 2006). This does not detract from the findings of Jones et al. (1999) that many larvae circulate then return to the reef of origin. Substantial evidence exists
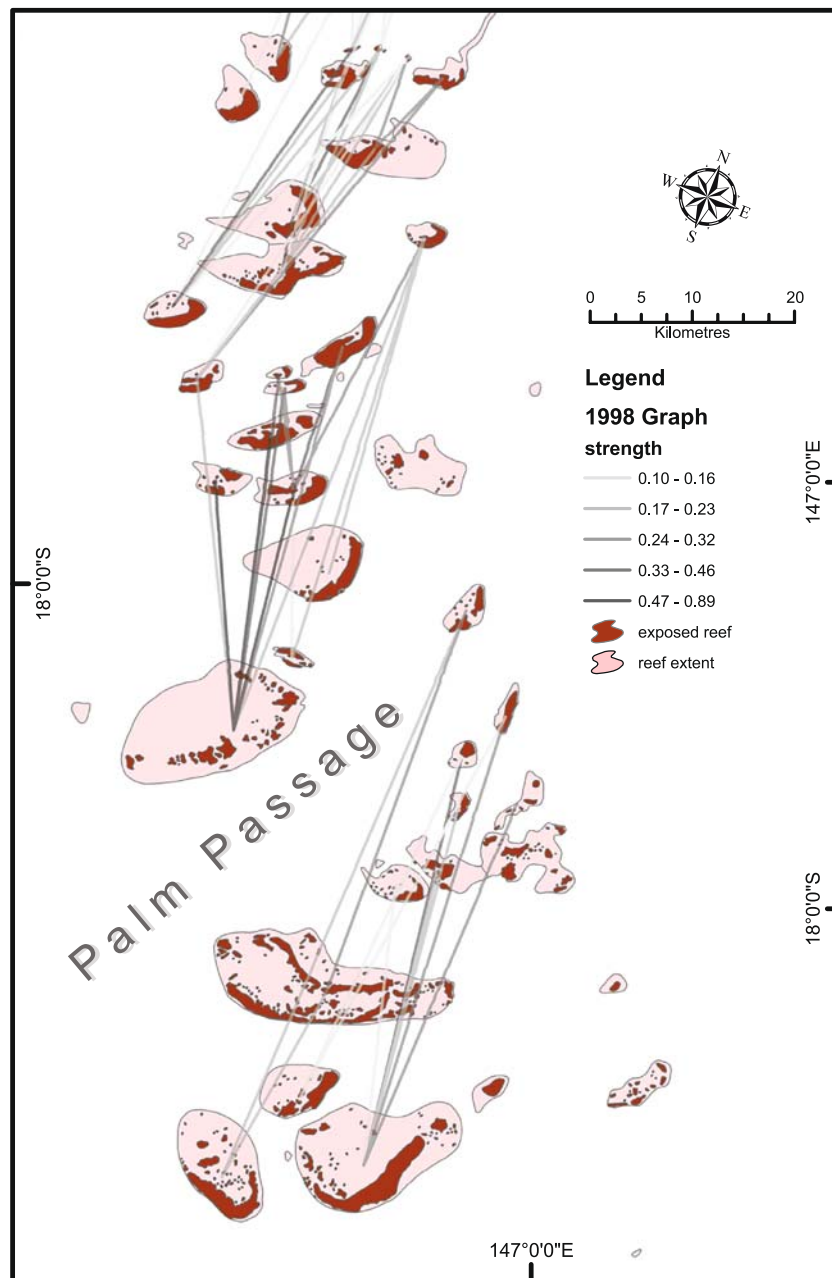
Fig. 12 Map showing connecting edges, with weights greater than 0.10, for the reefs near Hinchinbrook Island (−18 S, 146.5 E)

that planktonic larvae are found outside the local dispersal zone (Mora et al. 2003), and this could provide the mechanism to link populations in the GBR (Ayre and Hughes 2000). The contribution that each reef makes to GBR ecology needs to be evaluated in the context of the wider network. This network can be simulated by a hydrological model, such as James et al. (2002). Constraining the relationships between reefs to latitudinal and longitudinal descriptors will disregard the intergenerational connections that can serve to connect or, when absent, isolate populations (Barber et al. 2000; Bode et al. 2008).

Our conclusion that the GBR is a small-world system presents the largest known ecological network that exhibits high levels of connectivity combined with tight clustering. The implications for GBR conservation and scientific research are significant because understanding the metapopulation structure underpins our understanding of coral reef function. Exactly how this new understanding would explicitly change where we place no-take marine protected areas in any rezoning of the Great Barrier Reef is an important avenue for future research.

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