

Movement patterns of two carangid species in inshore habitats characterised using network analysis

Elodie J. I. Lédée^{1,2,*}, Michelle R. Heupel^{1,3}, Andrew J. Tobin¹, Amos Mapleston¹, Colin A. Simpfendorfer¹

¹Centre for Sustainable Tropical Fisheries and Aquaculture, College of Marine and Environmental Sciences, James Cook University, Townsville, QLD 4811, Australia

²AIMS@JCU, Australian Institute of Marine Science, College of Marine and Environmental Sciences, James Cook University, Townsville, QLD 4811, Australia

³Australian Institute of Marine Science, PMB No. 3, Townsville MC, Townsville, QLD 4810, Australia

ABSTRACT: Carangids are important ecological components of coastal and reef habitats, in addition to their economic significance as a target species for some fishers. Despite these important ecological and economic roles, little information is available on the movement ecology of these species. Passive acoustic monitoring was used to track the movements of 16 giant trevally *Caranx ignobilis* and 20 golden trevally *Gnathanodon speciosus* in Cleveland Bay off the coast of Queensland, Australia. Long-term observations of behaviour and movement were recorded via a network of acoustic receivers, and a network analysis approach (a novel, alternative approach to conventional movement analysis) was applied to the collected data. Tagged individuals were present in the study region between 30 and 394 d (mean \pm SD: 166 \pm 116 d) with a mean \pm SE residency index of 0.7 \pm 0.1. Notable inter-annual variation occurred with individuals that were detected on more days and more receivers, moved more frequently, and were more resident in some years than in others. In addition, movement patterns differed between species, with *C. ignobilis* being detected on fewer days by fewer receivers and moving less than *G. speciosus*. Network analysis revealed that a combination of factors including ontogeny, foraging niche, and habitat influences may explain differences in space use between the species. These results highlight unique behaviours between co-occurring and closely related species and enhance our understanding of animal interactions in inshore habitats.

KEY WORDS: Acoustic monitoring · *Caranx ignobilis* · *Gnathanodon speciosus* · Information theoretic approach · Network analysis · Mixed model effects

— Resale or republication not permitted without written consent of the publisher —

INTRODUCTION

Coastal waters are important fish habitats with high diversity and abundance (Allen et al. 2006, Tobin et al. 2014), but are highly dynamic with major fluctuations in environmental conditions at a variety of spatial and temporal scales (James et al. 2007, Knip et al. 2010). Tides, rainfall, salinity and wind are among the physical factors influencing animal move-

ments in the coastal environment (Allen et al. 2006, Knip et al. 2010). For example, tropical bays experience increased freshwater input during summer, which in turn decreases salinity and temperature in areas around river mouths and causes species to move out of the area (Allen et al. 2006, Knip et al. 2010). Coastal waters also provide a range of ecological services for both juvenile and adult fish; including nursery grounds, spawning and foraging areas,

*Corresponding author: elodie.ledee@my.jcu.edu.au

and refuge from predators (Knip et al. 2010, Tobin et al. 2014). As a result, some species occupy coastal areas based on seasonal or ontogenetic influences. In contrast, despite environmental fluctuations and life history changes, many species use coastal habitats year-round. Thus, movement and habitat use patterns within coastal habitats can be complex and dynamic (Langton et al. 1996, Stoner et al. 2001), and understanding the factors driving these patterns at specific spatial and temporal scales is critical for interpreting species ecology (Roessig et al. 2004, Andrews & Harvey 2013). Due to close proximity to human development, understanding species' movement and habitat use within coastal habitats is essential for assessing their vulnerability to anthropogenic threats and the efficacy of management strategies (Halpern et al. 2008, Knip et al. 2012a).

Network analysis is emerging as a powerful tool for assessing marine animal movement and habitat use (e.g. Jacoby et al. 2012, Mourier et al. 2012, Espinoza et al. 2015, Lédée et al. 2015a, Stehfest et al. 2015) and providing useful information for management and conservation. However, few studies have used network analysis to analyse animal movement in response to changes in biological and environmental factors (Wittmyer et al. 2005, Espinoza et al. 2015, Wilson et al. 2015). Network analysis examines the interactions between animals and their environment represented as a network characterized by connections (or edges) between nodes (West 2001). Applied to acoustic monitoring, nodes represent acoustic receivers (i.e. habitat patches) and edges represent movement of an individual between nodes (Jacoby et al. 2012, Lédée et al. 2015a). Complementary information about the physical or environmental attributes of the area can also be added to the node and edge properties. Consequently, network analysis can be adapted to various situations and scales (Croft et al. 2008, Stehfest et al. 2013). It also provides numerous metrics to address the different characteristics of animal movement within a network that are not provided by other methods. For example, the density of a network provides information on route selection within that network (Lédée et al. 2015a); an individual has more routes to select from in a densely connected network. Therefore, network analysis may be useful for analysing animal movement patterns in a variable environment, such as in coastal habitats.

Carangidae are an abundant and ecologically important family that includes ~150 species (Nemeth 2012), many of which are found in coastal tropical waters (Blaber & Cyrus 1983). Carangid species

occupy various habitats, from estuarine and shallow inshore reefs to offshore reefs and oceanic waters (Gunn 1990), and are one of the most important commercial fishes, although their economic value varies across tropical regions. Despite their abundance, ecological importance and economic value, the biology and ecology of carangids are poorly studied, with little information available on their spatial ecology (Wetherbee et al. 2004, Lédée et al. 2015b). The 2 most common carangids caught in northern Australia are giant trevally *Caranx ignobilis* and golden trevally *Gnathanodon speciosus* (Taylor et al. 2012), however, both species have received little attention in the scientific literature (but see Sudekum et al. 1991, Wetherbee et al. 2004). General information on distinctive characters, size and distribution is known, but information on reproduction, movement patterns and habitat use is limited. Therefore, information on the ecology and movement of these species will help to define their role in the ecosystem and manage their use. The aims of this study were (1) to develop methodologies for assessing the environmental drivers of movement via network analysis, (2) to examine and compare movement patterns of these 2 carangid species in coastal environments, and (3) to define temporal changes in network metrics and determine the role of biological and environmental drivers in affecting these metrics.

MATERIALS AND METHODS

Study site

Cleveland Bay on the northeast coast of Queensland, Australia, is a shallow embayment (<10 m depth) covering an area of ~225 km² (Fig. 1). The bay has varied habitats including coral reef, sand banks, intertidal mudflats, seagrass beds and mangrove forests (Munroe et al. 2015) and is influenced by tides ranging up to 4.2 m. The main sources of freshwater input are located on the southeastern side of the bay and provide seasonal freshwater input (Knip et al. 2011). Acoustic monitoring was used to track 2 carangid species, *Caranx ignobilis* and *Gnathanodon speciosus*, between 2011 and 2014. Acoustic receivers (VR2W Vemco; n = 65); divided between the western (n = 28) and eastern (n = 37) sections of the bay (Fig. 1) were deployed to track fish movements (see Knip et al. [2011] for a detailed description of receiver deployment methodology). The receivers were deployed on average 2 km apart and had a detection range of ~500 m within Cockle Bay (Fig. 1,

Chin et al. 2016) and ~900 m for the remaining areas of Cleveland Bay (Knip et al. 2012b), so there was limited overlap in detection ranges. Receiver data were downloaded quarterly.

Acoustic monitoring and fish tagging

Fishing effort was concentrated in areas frequented by *C. ignobilis* and *G. speciosus* based on local knowledge. Individuals were captured using fly rods, rod and reels and gillnets. Fly rods were rigged with artificial flies and rod and reels with artificial lures; barbs on hooks were flattened to reduce tissue damage during capture. Bottom-set gillnets (11 cm stretched mesh) were deployed for approximately ~1 h and checked every 15 min to allow for tagging and release of fish in optimal condition. After capture, individuals were placed in a large water-filled bin containing Aqui-S (AQUI-S New Zealand) diluted with seawater (1:10 000) from the study site (~35 ppt) and surgically fitted with a 9 × 29 mm acoustic transmitter (V9-2x, Vemco). Acoustic transmitters were implanted in the body cavity to ensure long-term retention. Incisions were closed with 2 running stitches using disposable needles and Polydioxanone monofilament absorbable sutures. The transmitters emitted a coded acoustic signal at 69 kHz with a pseudo-random ping rate between 50 to 130 s and an estimated battery life of 405 d. After surgery, individuals were measured to the nearest cm fork length, tagged with an external identification tag, and a fin clip was taken for species identification. Individuals were retained for a maximum of 10 min during tagging and measuring procedures. Species identification was confirmed using the COI gene sequence obtained following the method of Persis et al. (2009) and compared against known sequences in GenBank.

Environmental data

Environmental data were obtained from 4 different sources. Air temperature (°C), barometric pressure (hPa), wind speed (km h⁻¹), wind direction (°), rainfall accumulation (ml) and solar exposure (MJ m⁻²) were sourced from the Bureau of Meteorology of Australia (www.bom.gov.au/). Wind data was transformed into 2 variables: alongshore (north-south) and cross-shore (east-west) winds fol-

lowing the method of Begg et al. (2006; p. 44). Solar exposure (referred to as light intensity) was the total solar energy for 1 d (midnight to midnight). Moon illumination (luminosity) was sourced from the United States Naval Observatory (<http://aa.usno.navy.mil/data/docs/MoonFraction.php>). Freshwater flow (l m⁻¹) from Alligator Creek was sourced from the Department of Natural Resources and Mines (<http://water-monitoring.information.qld.gov.au>). Water temperature (°C) was sourced from an Australian Institute of Marine Science (AIMS) weather station in Cleveland Bay (AIMS 2015). Environmental data were recorded at a variety of temporal scales, and mean values were aggregated by season and year (year-season) and by month and year (year-month) (Fig. S1 in Supplement 2 at www.int-res.com/articles/suppl/m553p219_supp.pdf) for analyses of movement.

Data analysis

Detection data for each individual were exported from a VUE database (Vemco) and analysed in the R statistical environment (R Development Core Team 2014) with the igraph package (Csardi & Nepusz

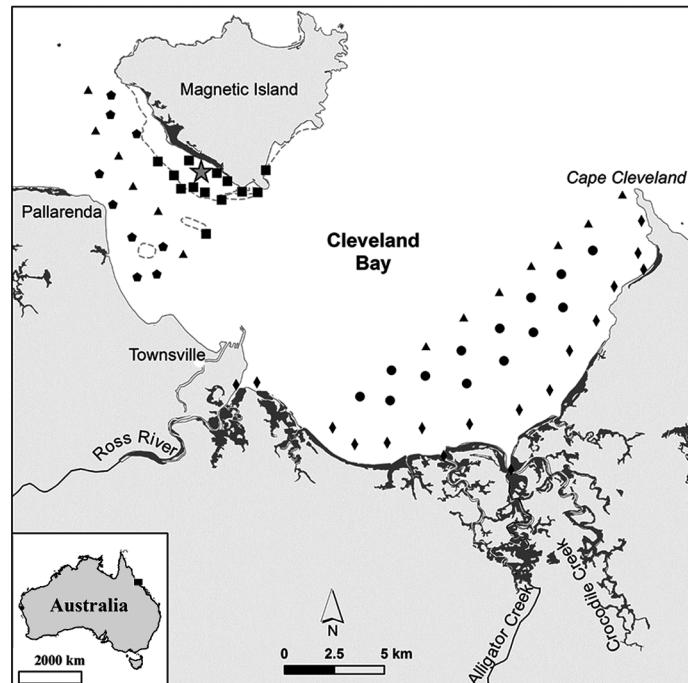


Fig. 1. Study site in Cleveland Bay, Queensland, Australia (see inset). Receiver locations in deeper areas (triangle), mudflats (diamond), coral reefs (square), sandy bottoms (pentagon) and seagrass beds (circle). Reefs (light grey dashes) and mangrove forests (dark grey shading) are also indicated. Cockle Bay location (star)

2006). Only individuals detected in the study area for 2 wk or more were analysed, to ensure all individuals had sufficient data to support the analysis approaches applied. Detection data were used to create square matrices that counted individual presence at, and relative movements between, acoustic receivers within the bay. Detections at the same receiver were filtered using a 5 min interval. Relative movement was defined as the number of times an individual moved between 2 receivers, divided by the total number of movements made by the individual within its activity space (i.e. total number of edges in the network, Jacoby et al. 2012). Square matrices were used to create directed and weighted networks which represented individual activity space in Cleveland Bay. Each network was tested for non-random patterns using a link rearrangement (i.e. permutation) and bootstrap approach ($n = 10\,000$; Croft et al. 2011). The observed movements were randomly shuffled between receivers and new networks were generated using the same degree distribution as the original network (i.e. the procedure randomized the link while maintaining the degree distribution of the network). For each random network, metrics were calculated and compared to metrics from the observed network using coefficient of variation and likelihood ratio tests (χ^2 , $p < 0.05$).

Movement data were assessed seasonally and monthly for each year by constructing networks for individual fish. The number of receivers and paths, relative movements (see previous paragraph), average path length, network cluster, network diameter and network density were calculated for each network. A path was a route between 2 receivers in the network. Average path length (APL) was a measure of reachability within the network (Rayfield et al. 2011). Network cluster identified sub-networks of interconnected receivers that were closer to each other than to other receivers in network space (Rayfield et al. 2011). Network diameter was an indicator of the size of the network (Urban & Keitt 2001) while network density measured route selection (ranging from 0 to 1). A residency index was calculated for each individual by dividing the number of days an individual was detected within the study area by the days at liberty (i.e. from the time of first detection to the time of last detection). The difference in the number of detections, receivers, paths and movements, residency index, network diameter, network cluster, APL and network density between species, fork length and year of deployment was tested using ANCOVA. Post-hoc multiple comparisons (Tukey's

HSD, $\alpha = 0.05$) were used to define differences between species and year of deployment where significant differences were detected.

Linear mixed effects models (LMM) were used to investigate the influence of environmental data, fork length and region of the bay (i.e. east or west side, for *C. ignobilis* only) on the network metrics (e.g. average path length, network density, network diameter and network cluster; see Supplement 1 at www.int-res.com/articles/suppl/m553p219_supp.pdf for a detailed description of the analyses). In each case, fixed factors (i.e. predictors) were centered to simplify interpretation and facilitate comparison of their importance (Schielzeth 2010). A variable (ID_YR) combining individual tag and year was included as a random factor to enable population-level prediction, account for the repeated-measures nature of the data and for unequal numbers of detections used to construct individual networks across years (Bolker et al. 2009). Linear models were implemented using the lme function from the nlme package (Pinheiro et al. 2014) in the R statistical environment (R Development Core Team 2014). Collinearity between factors was assessed using variance inflation factors (VIF; R package 'car'; Fox & Weisberg 2011). Barometric pressure was not included in any of the year-season and year-month global models based on VIF values, due to collinearity with water temperature. Rainfall accumulation, freshwater flow and light intensity were not included in any of the year-season global models based on VIF values, due to collinearity with each other and water temperature. Light intensity was not included in the *G. speciosus* monthly APL global models based on VIF values, due to collinearity with rainfall accumulation. Moon illumination was not included in the LMM monthly analysis as it was not informative at a monthly scale. Data (i.e. response) normality was also tested prior to statistical analysis and data was transformed to normality when required. Fixed factors and interactions were examined using the residualPlots function (R package 'car'; Fox & Weisberg 2011); interactions were only considered if the Tukey test (an output of the residualPlots function) was significant ($p < 0.05$; Zar 1999).

Multi-model inference using an information theoretic approach was used to investigate the effects of fish size and environmental factors on seasonal and monthly network metrics for each species. Diagnostics plots (i.e. residuals plot and auto-correlation function plot) were used to evaluate goodness of fit (Burnham & Anderson 2002, Zuur et al. 2010). If auto-correlation was present, global models were fitted with different correlation functions to account for temporal auto-

correlation and heteroscedasticity. The corrected Akaike's information criterion (AIC_c) was recalculated and final models with the lowest AIC_c values were selected for analyses (see Supplement 1). A set of nested models with different combinations of fixed variables was derived from global models (Johnson & Omland 2004, Bolker et al. 2009) using the dredge function from the MuMIn package (Barton 2014). The best nested models ($\Delta AIC_c < 2$) were compared against the null model: $y \sim 1 + (1 | ID_YR)$, where y is the response and ID_YR the random factor, and significant differences were evaluated with maximum likelihood ratio tests (χ^2 , $p < 0.05$). Fixed factor estimates were calculated using the model.avg function from the MuMIn package to determine their relative importance and account for model selection uncertainty (Johnson & Omland 2004, Grueber et al. 2011). The full model-averaged coefficients (i.e. shrinkage estimates) were used to account for nested model selection bias (Burnham & Anderson 2002).

Differences in year-season and year-month APL, density, diameter and cluster between bay regions (east vs. west side, for *C. ignobilis* only) were examined independent of other environmental factors to remove correlation effects and reduce complexity of mixed-effect models. Wald Z-tests were used to determine overall bay region effect compared to the null model.

RESULTS

Movement data were examined from 16 *Caranx ignobilis* (2013: $n = 7$; 2014: $n = 9$) and 20 *Gnathanodon speciosus* (2011: $n = 10$; 2012: $n = 1$; 2013: $n = 9$) acoustically monitored in Cleveland Bay. All individuals were successfully identified as *C. ignobilis* and *G. speciosus* by COI gene sequencing, with

>98% similarity to sequences previously submitted to GenBank. The first 2 d of data after release were removed to obtain representative samples and allow individuals sufficient time to return to normal behaviour. Individual fish removed from the analyses comprised 3 *C. ignobilis* and 8 *G. speciosus* that were not detected and 3 *C. ignobilis* and 3 *G. speciosus* that were detected for <15 d. The remaining ($n = 19$) individuals were only detected in the region of the bay (east or west) in which they were caught. Individual size ranged from 33 to 80 cm (fork length [FL]; mean \pm SD = 46 ± 13 cm) and size differed between species ($F_{1,14} = 169.1$, $p < 0.001$) with *C. ignobilis* on average smaller (37.2 ± 4.3) than *G. speciosus* (56.5 ± 11.6). In addition, *C. ignobilis* on the east side of Cleveland Bay were significantly smaller (34.9 ± 2.0) than *C. ignobilis* on the west side (39.6 ± 4.8 ; $F_{1,6} = 18.78$, $p < 0.005$). *C. ignobilis* reach maturity between 55 and 65 cm FL (Wetherbee et al. 2004) so all were likely to be juvenile at the time of capture (Table 1). *G. speciosus* reaches maturity at ~33 cm FL (Grandcourt et al. 2004); consequently, all individuals were likely to be adults at the time of capture.

Individuals were present in Cleveland Bay for 30 to 394 d (mean \pm SD = 166 ± 116 d; Fig. 2) with a mean residency index of (mean \pm SE) 0.7 ± 0.1 (Table S2 in Supplement 2 at www.int-res.com/articles/suppl/m553p219_supp.pdf). Residency did not differ between species (Table 2), but *C. ignobilis* residency index was significantly lower on the east side of the bay compared to the west side ($F_{1,7} = 91.6$, $p < 0.001$). On average, *G. speciosus* were detected by twice as many receivers, had 4 times as many paths, and moved within their networks seven-fold more than *C. ignobilis* during the study period (Table 1). *C. ignobilis* and *G. speciosus* were detected on more days and more receivers, moved more frequently, were more resident and had smaller networks in 2013 than

Table 1. Network metrics for *Caranx ignobilis* and *Gnathanodon speciosus* in Cleveland Bay from 2011 to 2014. Values are mean \pm SD (fork length, receivers, path and movement) or mean \pm SE (average path length, network density, network diameter and network cluster). The Cleveland Bay array comprised 65 receivers

Period	Fork length (cm)	Receivers	Path	Movement	Average path length	Network density	Network diameter	Network cluster
<i>C. ignobilis</i>								
Year-season	37 ± 4	4.2 ± 1.2	4.7 ± 2.8	31.8 ± 34.4	1.48 ± 0.06	0.60 ± 0.04	0.27 ± 0.03	0.38 ± 0.06
Year-month		3.4 ± 1.2	3.3 ± 2.2	18.8 ± 28.1	1.42 ± 0.05	0.66 ± 0.03	0.37 ± 0.04	0.48 ± 0.06
Overall		6.6 ± 1.7	10.2 ± 4.9	103.6 ± 101.1	1.79 ± 0.10	0.44 ± 0.03	0.04 ± 0.02	0.5 ± 0.07
<i>G. speciosus</i>								
Year-season	57 ± 12	8.1 ± 4.3	15.3 ± 12.0	152.2 ± 214.4	1.93 ± 0.12	0.45 ± 0.03	0.13 ± 0.02	0.46 ± 0.03
Year-month		7.2 ± 3.3	11.6 ± 8.1	80.4 ± 89.1	1.94 ± 0.07	0.42 ± 0.02	0.16 ± 0.02	0.35 ± 0.02
Overall		13.1 ± 5.4	36.3 ± 21.9	754.9 ± 706.9	1.89 ± 0.12	0.39 ± 0.4	0.01 ± 0.00	0.67 ± 0.04



Fig. 2. Presence plot of *Caranx ignobilis* and *Gnathanodon speciosus* individuals ($n = 25$) detected in Cleveland Bay by day from February 2011 to November 2014; y-axis labels indicate tag ID and fork length (cm). Non-shaded area: *Caranx ignobilis* individuals; shaded area: *Gnathanodon speciosus* individuals

Table 2. Statistical comparison (ANCOVA) of network metrics between year of individual fish release (YR), species (*Caranx ignobilis* and *Gnathanodon speciosus*) and fork length. Asterisks indicate significant effect ($p < 0.05$)

Metric	Factor	df	F	p
Detection number	YR	2,13	26.95	<0.001*
	Species	1,13	11.78	<0.001*
	Fork length	1,13	0.89	0.36
Detection days	YR	2,14	5.56	0.02*
	Species	1,14	10.35	0.006*
	Fork length	1,14	0.66	0.43
Residency index	YR	2,13	24.33	<0.001*
	Species	1,13	1.91	0.19
	Fork length	1,13	0.04	0.84
Receiver	YR	2,10	5.65	0.02*
	Species	1,10	39.04	<0.001*
	Fork length	1,10	1.65	0.22
Path	YR	2,11	2.33	0.14
	Species	1,11	84.61	<0.001*
	Fork length	1,11	4.93	0.05
Movement	YR	2,13	32.75	<0.001*
	Species	1,13	69.42	<0.001*
	Fork length	1,13	0.91	0.36
Average path length	YR	2,13	3.31	0.07
	Species	1,13	0.06	0.81
	Fork length	1,13	3.66	0.08
Network density	YR	2,13	2.77	0.1
	Species	1,13	0.21	0.65
	Fork length	1,13	0.39	0.54
Network diameter	YR	2,14	26.03	<0.001*
	Species	1,14	18.46	<0.001*
	Fork length	1,14	0.12	0.73
Network cluster	YR	2,12	0.79	0.48
	Species	1,12	6.23	0.03*
	Fork length	1,12	0.31	0.59

in 2014, and in 2011 than in 2013, respectively (Table 2). In addition, movement patterns significantly differed between species, with *C. ignobilis* detected on fewer days, fewer receivers, moving less and having larger networks and fewer network clusters than *G. speciosus* across all years (Table 2). There was no difference in the within-region movement patterns of *C. ignobilis* between the bay regions, which allowed for comparison between species at the bay level. There was no significant effect of individual length on tested metrics (Table 2).

Seasonal networks

For 91.4 % of *C. ignobilis* (32 networks from 10 individuals) and 100.0 % of *G. speciosus* (48 networks from 9 individuals) year-season networks, there was no evidence of random movement (permutation tests; χ^2 , $p < 0.001$; Fig. 3). The random networks were excluded from subsequent analyses. *G. speciosus* year-season networks contained twice as many receivers and at least 3 times as many paths and movements than *C. ignobilis* (Table 1). Year-season network metrics were significantly different between species (Table 3a), with *G. speciosus* having a smaller network diameter and less dense networks with a higher number of network clusters and longer APLs compared to *C. ignobilis* (Table 1), indicating that *G. speciosus* seasonal activity space was smaller and patchier.

Two APL and 3 network density nested models for *C. ignobilis* best fit the data ($\Delta\text{AIC}_c < 2$). All but one of the network density models were significantly better than the null model ($p < 0.05$) (Table S3a,b in

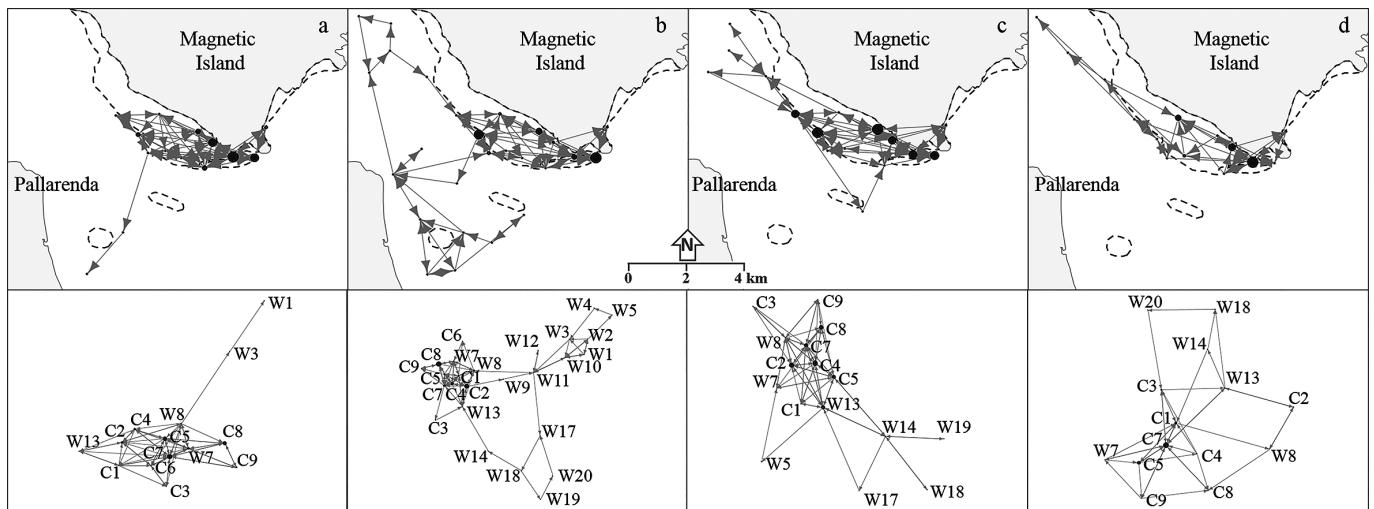


Fig. 3. *Gnathanodon speciosus* seasonal networks within the western side of Cleveland Bay in 2011. (a) Autumn, (b) winter, (c) spring and (d) summer. Top panels are the geographic and bottom panels the Fruchterman-Reingold representations (Fruchterman & Rheingold 1991) of year-season networks. Size of node (filled circles) represents the relative filtered number of detections at the acoustic receivers. Node label indicates the name of the acoustic receiver. A path between 2 acoustic receivers is represented by a grey arrow. Reefs (dark grey dashes) are also indicated

Supplement 2). All 5 nested models included fork length as a fixed variable explaining 75 % of relative importance, however, the effect of fork length was not substantial, as <33 % of APL and network density estimates showed a relationship with fork length (Table S4a,b in Supplement 2). Null models were included in the best-fitted nested models for *C. ignobilis* network diameter (only 1 model) and network clusters. None of the network cluster models were significantly better than the null model (χ^2 , $p > 0.05$) (Table S3c,d). There was no significant effect of bay region ($p > 0.05$; Table S5a in Supplement 2), fork length or environmental data (Table S4) on *C. igno-*

Table 3. *Caranx ignobilis* and *Gnathanodon speciosus* differences on (a) seasonal and (b) monthly average path length (APL), network density (Den), network diameter (Dia) and network cluster (Clus) in Cleveland Bay. Asterisks indicate significant effect ($p < 0.05$) using the Wald Z and chi-squared tests

Model	χ^2	df	p
(a) Seasonal			
APL ~ Species	3.9	1	0.048*
log(Den) ~ Species	10.9	1	0.002*
Dia ~ Species	23.0	1	<0.001*
sqrt(Clus) ~ Species	5.2	1	0.02*
(b) Monthly			
APL ~ Species	40.4	1	<0.001*
Density ~ Species	36.9	1	<0.001*
log(Dia) ~ Species	6.9	1	0.009*
Cluster ~ Species	0.2	1	0.66

bilis year-season network metrics, indicating that none of these factors were important drivers of *C. ignobilis* network metrics at a seasonal level.

All *G. speciosus* best mixed effects nested models ($\Delta\text{AIC}_c < 2$) were significantly better than the null model ($p < 0.05$; Table S6 in Supplement 2). Five fixed variables were present in most of the models: fork length, cross-shore wind, water temperature, alongshore wind and moon illumination; but only fork length, alongshore wind and moon illumination had significant effects on network metrics (Table 4). The mixed-effects model showed that APL was influenced by fork length (Table 4a) with *G. speciosus* year-season networks having longer APLs as fork length increased (Fig. 4a). *G. speciosus* year-season networks revealed denser networks as alongshore wind increased (more northerly wind; Fig. 4b, Table 4b). Fork length and environmental data were not found to influence the diameter of *G. speciosus* year-season networks (Table 4c). Finally, the effect of moon illumination was significant (Table 4d) on the level of *G. speciosus* year-season network clustering; with higher illumination leading to more year-season networks with fewer clusters (Fig. 4c).

Monthly networks

For 90.3 % of *C. ignobilis* (56 networks from 10 individuals) and 99.0 % of *G. speciosus* (97 networks from 9 individuals) year-month networks there was

Table 4. Environmental and fish size effects on *Gnathanodon speciosus* seasonal network metrics from model-averaging analysis. Environmental parameters were standardised for comparison. Asterisks indicate significant effect ($p < 0.05$) on seasonal network metrics of *G. speciosus* in Cleveland Bay. NA: not applicable

	Estimate ± SE	<i>z</i>	<i>p</i>	Relative importance
(a) Average path length				
(Intercept)	0.000 ± 0.000	NA	NA	–
Fork length	0.462 ± 0.194	2.381	0.017*	0.95
Cross-shore wind	0.152 ± 0.184	0.824	0.410	0.55
Water temperature	-0.162 ± 0.196	0.826	0.409	0.56
Moon illumination	0.105 ± 0.172	0.611	0.541	0.42
Alongshore wind	-0.065 ± 0.138	0.467	0.640	0.33
(b) Network density				
(Intercept)	0.000 ± 0.000	NA	NA	–
Moon illumination	-0.124 ± 0.117	1.061	0.289	0.62
Alongshore wind	0.509 ± 0.143	3.554	<0.001*	0.96
Fork length	-0.017 ± 0.065	0.261	0.794	0.15
Water temperature	0.037 ± 0.100	0.370	0.712	0.22
Cross-shore wind	-0.015 ± 0.098	0.156	0.876	0.16
(c) Network diameter				
(Intercept)	0.000 ± 0.000	NA	NA	–
Fork length	-0.324 ± 0.202	1.601	0.109	0.84
Moon illumination	0.213 ± 0.192	1.106	0.269	0.70
Cross-shore wind	0.294 ± 0.191	1.544	0.123	0.84
Alongshore wind	-0.110 ± 0.163	0.674	0.500	0.46
Water temperature	-0.073 ± 0.137	0.533	0.594	0.35
(d) Network cluster				
(Intercept)	0.000 ± 0.000	NA	NA	–
Moon illumination	-0.391 ± 0.132	2.959	0.003*	0.98
Cross-shore wind	-0.302 ± 0.214	1.411	0.158	0.78
Alongshore wind	0.164 ± 0.154	1.066	0.287	0.64
Water temperature	0.007 ± 0.118	0.058	0.954	0.29
Fork length	-0.018 ± 0.067	0.268	0.788	0.16

no evidence of random movement based on the results of the permutation tests (χ^2 , $p < 0.001$). *G. speciosus* year-month networks included twice as many receivers and >3 times as many paths and movements than *C. ignobilis* networks (Table 1). Year-month network metrics were significantly different between species (Table 3b), with *C. ignobilis* having larger (i.e. network diameter) and denser networks, and a longer APL compared with *G. speciosus* (Table 1); indicating that at a monthly level, *C. ignobilis* activity space was larger and more complex.

Null models were included in the best-fitted nested models for all *C. ignobilis* year-month network metrics (Table S7 in Supplement 2). None of the APL, network diameter and network cluster nested models were significantly better than the null model (χ^2 , $p > 0.05$) (Table S7a,c,d), however, 6 of the network density nested models were significantly better than the null model (χ^2 , $p < 0.05$) (Table S7b). All 6 models included cross-shore wind as a fixed factor (Table S7b)

with a relative importance of 88%; but the effect was not significant. Interestingly, cross-shore wind was also included in all the year-month network metrics models (APL, network diameter and network cluster; Table S7a,c,d), but its relative importance was less than 66% (Table S8a,c,d in Supplement 2) and effects were not significant. Finally, there was no significant effect of bay region ($p > 0.05$) (Table S4), fork length or environmental data (Table S8) on *C. ignobilis* year-month network metrics; indicating that none of the predictors had a significant effect on *C. ignobilis* year-month activity space.

All *G. speciosus* best mixed-effects nested models ($\Delta\text{AIC}_c < 2$) for 3 monthly network metrics (i.e. APL, network diameter and network cluster) were significantly better than the null model ($p < 0.05$) (Table S9 in Supplement 2). Five fixed variables were present in most of the models: fork length, alongshore wind, water temperature, light intensity and rainfall accumulation; but only alongshore wind, fork length and light intensity had significant effects, on 2 network metrics (Table 5). APL was influenced by alongshore wind (Table 5a) with *G. speciosus* year-month networks having shorter APLs as alongshore wind increased (Fig. 4d). Model averaging

showed fork length and light intensity significantly influenced the diameter of *G. speciosus* year-month networks (Table 5c), with increased network size as fork length increased and light intensity decreased (Fig. 4e,f). There was no significant effect of fork length or environmental data on the clustering of *G. speciosus* year-month networks (Table 5d). Finally, none of the *G. speciosus* network density models were significantly better than the null model (χ^2 , $p > 0.05$) (Table S9b) indicating neither fork length nor environmental data were influential (Table 5b).

DISCUSSION

Network analysis revealed that environmental drivers affected the movement of the 2 carangid species differently. Several environmental drivers significantly affected the movement patterns of *Gnathanodon speciosus*, but had little or no effect on

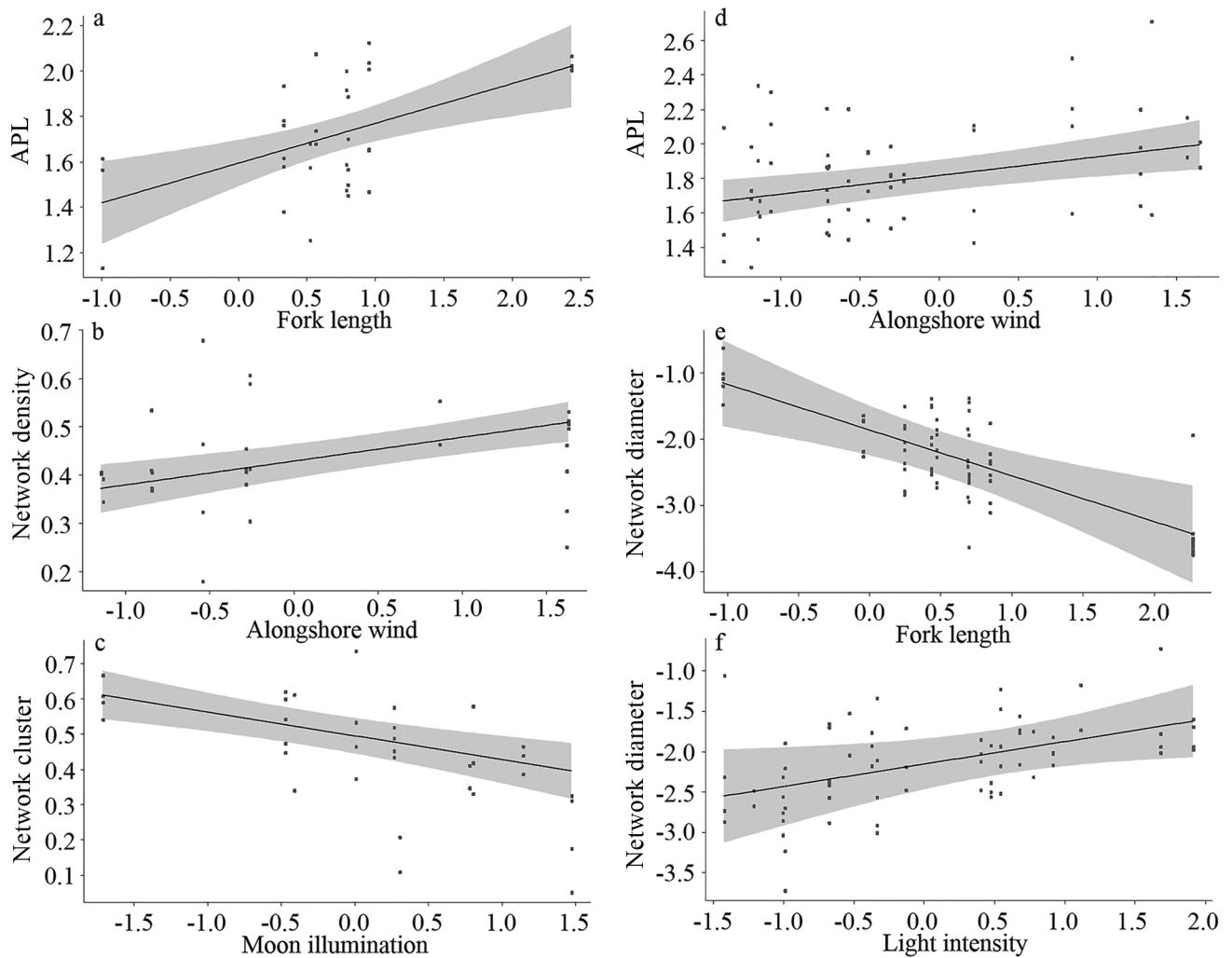


Fig. 4. Fish size and environmental effects on (a,d) average path length (APL), (b) network density, (c) network cluster and (e,f) network diameter metrics of *Gnathanodon speciosus* in (a–c) seasonal and (d–f) monthly networks

Caranx ignobilis movement patterns. Use of 4 network metrics provided insight into a range of movement attributes of these species and how environmental drivers affected those attributes. Network diameter (a proxy for the amount of space used) and network cluster (an indication of differences in patterns of use; i.e. patchy space use) provided a general description of the networks. APL (reachability) and network density (route selection) provided information on individual movement within networks, indicating how regularly parts of the individual's network were visited and how specific the routes were. The latter 2 metrics provided information about movement within activity spaces that is not provided by traditional home range methods. These results align with previous studies that highlight the potential advantages of using network analysis in animal

movement studies to obtain a comprehensive picture of individual movement. Network analysis can be used to either simply visualise animal movement pathways and changes in activity space (Jacoby et al. 2012, Finn et al. 2014), or to investigate more complex aspects of space use (Lédée et al. 2015a), determine structural and functional connectivity (Kinmonth et al. 2010, Espinoza et al. 2015) or model the movement of individuals (Stehfest et al. 2015, E. J. I. Lédée unpubl. data).

Tracking *C. ignobilis* and *G. speciosus* within the same location enabled comparison of their spatial ecology. Movement patterns differed between these 2 congeneric species. Despite being on average physically larger and at a later life stage, *G. speciosus* had smaller and more complex networks than *C. ignobilis*. Larger individuals generally exploit more

Table 5. Environmental and fish size effects on *Gnathanodon speciosus* monthly network metrics from model-averaging analysis. Environmental parameters were standardised for comparison. Asterisks indicate significant effect ($p < 0.05$) on monthly network metrics of *G. speciosus* in Cleveland Bay. NA: not applicable

	Estimate ± SE	z	p	Relative importance
(a) Average path length				
(Intercept)	0.000 ± 0.000	NA	NA	–
Alongshore wind	0.273 ± 0.132	2.066	0.039*	0.90
Water temperature	0.138 ± 0.159	0.866	0.387	0.55
Fork length	0.109 ± 0.167	0.655	0.513	0.44
Cross-shore wind	0.008 ± 0.047	0.164	0.870	0.22
Rainfall	0.009 ± 0.060	0.149	0.882	0.22
(b) Network density				
(Intercept)	0.000 ± 0.000	NA	NA	–
Water temperature	-0.072 ± 0.131	0.548	0.583	0.41
Light intensity	-0.047 ± 0.105	0.443	0.658	0.35
Alongshore wind	-0.039 ± 0.096	0.402	0.687	0.33
Rainfall	-0.021 ± 0.080	0.268	0.789	0.29
Cross-shore wind	-0.015 ± 0.065	0.227	0.821	0.26
Fork length	-0.017 ± 0.112	0.148	0.882	0.24
(c) Network diameter				
(Intercept)	0.000 ± 0.000	NA	NA	–
Fork length	-0.598 ± 0.202	2.966	0.003*	0.98
Light intensity	0.350 ± 0.124	2.817	0.005*	0.98
Rainfall	0.105 ± 0.109	0.956	0.339	0.64
Cross-shore wind	0.037 ± 0.071	0.519	0.604	0.39
Water temperature	0.114 ± 0.152	0.747	0.455	0.52
Alongshore wind	0.015 ± 0.051	0.286	0.775	0.27
(d) Network cluster				
(Intercept)	0.000 ± 0.000	NA	NA	–
Light intensity	-0.146 ± 0.155	0.938	0.348	0.61
Water temperature	-0.148 ± 0.182	0.815	0.415	0.54
Fork length	0.056 ± 0.136	0.413	0.680	0.32
Rainfall	0.021 ± 0.095	0.218	0.827	0.29
Alongshore wind	-0.037 ± 0.094	0.400	0.689	0.31
Cross-shore wind	0.010 ± 0.062	0.172	0.864	0.24

resources over larger areas, likely due to higher energy requirements and lower predation risk associated with travel (Gruss et al. 2011). Consequently, in our study the size of *G. speciosus* networks may be expected to be larger than those of *C. ignobilis* (Nash et al. 2015) due to the larger body size of *G. speciosus*. However, ontogeny, foraging strategies, and habitat use patterns may explain why *C. ignobilis* had larger networks than *G. speciosus* despite having shorter fork lengths. Both species feed on crustaceans, molluscs and fishes in sand (Grandcourt et al. 2004), but young *C. ignobilis* use a wider range of habitats, from brackish estuaries to shallow reefs (Sudekum et al. 1991, Wetherbee et al. 2004). In contrast, *G. speciosus* is commonly found on inshore reef and in deeper areas (Randall et al. 1997, Grandcourt et al. 2004), similar habitats to where *G. speciosus*

was found in the present study. These findings are consistent with other carangid species such as *C. ignobilis* and *C. orthogrammus* in Hawaii (Meyer et al. 2001), but more research on *C. ignobilis* and *G. speciosus* diet (e.g. using stable isotope analysis) should be undertaken to confirm these patterns.

The timing of the transmitter deployments may have also played a role in network differences. Although attempts were made to catch and track both species simultaneously, this was not feasible due to catch limitations. Both species were resident in the bay, which is similar to previous findings for adult *C. ignobilis* (Meyer et al. 2007, Lédée et al. 2015b) and other coastal predator species such as *C. melampygus* (Holland et al. 1996), *Carcharhinus sorrah* (Knip et al. 2012b) and *C. fitzroyensis* (Munroe et al. 2015). However, long-term residency patterns varied across individuals and bay regions, with some individuals not detected ~60% of the time. These individuals (55% of *G. speciosus* and 38% of *Caranx ignobilis*) may have been present in unmonitored portions of the bay or could have departed the area. Within-population variability may exist where a proportion of individuals display transient movement behaviour—a pattern common in other species such as *Lethrinus miniatus* (Currey et al. 2014), *Plectropomus leopardus* (Matley et al. 2015) and *Carcharhinus sorrah* (Knip et al. 2012b) and may reduce intra-specific competition for resources (Chapman et al. 2012). Consequently, mechanisms behind residency may be more complex and variable than the current analysis can explain.

G. speciosus showed distinct movement patterns during the study period related to environmental factors at seasonal and monthly time scales. Fork length was a significant factor in *G. speciosus* APL and network diameter which provided insight into reachability of sections within and the size of their network. As fork length increased, network size increased and sections of their network took longer to reach (i.e. higher APL). This result is consistent with other teleost (Nash et al. 2015) and shark (Heupel et al. 2004, Knip et al. 2011) studies that found space use of individuals increased with body size; which likely

reflects an increase in energy requirements associated with growth (Nash et al. 2015). Additionally, individuals revisited areas within their network with low regularity (i.e. higher APL) indicating *G. speciosus* did not have high fidelity to specific parts of their network but rather used various core areas. This behaviour is typical of fast-swimming predators (Nash et al. 2015). Results for *G. speciosus* in this study were similar to those for *C. ignobilis* in the central Great Barrier Reef (GBR) reefs (Lédée et al. 2015b) and *Sphyraena tiburo* in Florida, USA (Heupel et al. 2006), where individuals used core areas throughout their networks with some areas re-used over a few months. *G. speciosus* networks became denser and sections took longer to reach with more northerly wind. In shallow coastal areas, influences of wind on wave action, turbidity and localized water temperature (Clark et al. 1996) are more important than they are in deeper areas. Wind with a northerly component would result in the west side of Cleveland Bay being more sheltered, providing calmer and less turbid waters, in turn offering greater opportunities for a visual hunter like *G. speciosus* (A. Mapleton unpubl. data). Consequently, the movement patterns of *G. speciosus* may have reflected foraging advantages. Wind is also known to decrease the detection ability of acoustic receivers due to increased noise (Udyawer et al. 2013, Heupel & Simpfendorfer 2014) which may have affected detection efficiency on the east side of the bay, but had less influence in the west. Finally, as moon illumination and light intensity increased, *G. speciosus* networks were less patchy and smaller in size. An increase in light intensity provided an increase in visual acuity and prey encounter rate to visual predators (Mills et al. 1984, Puvanendran & Brown 2002) indicating movements of *G. speciosus* may be concentrated on less and smaller areas when light levels are high. As a visual hunter, light (i.e. solar or moon illumination) is likely to be important for a range of *G. speciosus* behaviours related to their survival. Environmental factors thus affected *G. speciosus* movement in a number of ways, and the use of network metrics proved useful in understanding how they moved within the study area and within their network.

In the present study, 55% of *G. speciosus* were either infrequently or never detected, which could be the result of individuals suffering mortality or moving to unmonitored areas (e.g. shipping channel in the middle of the bay or outside the bay), therefore, the results might reflect only a portion of the population. Undetected individuals were smaller on average (<53 cm) than resident individuals (>56 cm), suggest-

ing that spatial movement patterns may differ within the adult population and possibly by life stage. Juveniles are known to display 'piloting' behaviour in offshore areas (Randall et al. 1997, Gunn et al. 1999), which was not observed in inshore waters, indicating adult and juvenile movement patterns may be driven by different survival strategies. Also, the behavioural polymorphism exhibited by the adult population might be explained by partial migration, where a proportion of the adult population is resident while others exhibit preferences for alternative areas or more nomadic movement. This behavioural pattern has been reported in other species (e.g. *C. sorrah*: Knip et al. 2012b; *L. miniatus*: Currey et al. 2014) and may be due to different feeding strategies (Gruss et al. 2011, Chapman et al. 2012), but directed research on diet and foraging is needed to confirm this behavioural pattern.

Caranx ignobilis displayed less variable and less predictable movement patterns than *G. speciosus*. None of the biological (i.e. fork length), physical (i.e. bay side) or environmental factors were important drivers of *C. ignobilis* networks at the different temporal scales (months or seasons); indicating that movement patterns of juveniles were similar in both regions of the bay and not easily predicted. Results were consistent with adult *C. ignobilis* in the central GBR reefs (Lédée et al. 2015b), where biological and environmental factors had little or no influence on space use; however, these results differed from juvenile *C. ignobilis* in Hawaii (Wetherbee et al. 2004), which exhibited increased space use with increased fish size. Possible explanations for the differences in juvenile movement patterns in Cleveland Bay and in Hawaii may include differences in fish size sampled and biological and physical factors between the study areas. For instance, Wetherbee et al. (2004) tracked individuals across a much wider size range (14 to 44 cm FL) than we did in the present study (33 to 48 cm FL). Furthermore, Wetherbee et al. (2004) studied *C. ignobilis* using active tracking for up to 2 wk, whereas passive monitoring was used in the present study from a month to over a year.

Despite the lack of environmental drivers of movement, *C. ignobilis* movement was influenced by ontogeny. Most of the smaller *C. ignobilis* (<35 cm FL; 50% of individuals) were captured and detected on the eastern side of Cleveland Bay. The east side of the bay is subject to variations in salinity and turbidity due to proximity to rivers (Knip et al. 2011), and is similar to the estuarine environments generally favoured by smaller juvenile *C. ignobilis* (Wetherbee et al. 2004). In contrast, larger juveniles were found

on the western side of the bay near coral and sand habitats. In addition, no cross-bay movements were observed. These results suggest that areas on the eastern side of Cleveland Bay may serve as a nursery ground for smaller juvenile *C. ignobilis* before they shift to more reef-associated locations as they grow, resulting in the observed habitat partitioning by fish size. Ontogenetic migration is common in numerous teleost species (Gruss et al. 2011) and *C. ignobilis* spatial segregation by fish size is consistent with the findings of Wetherbee et al. (2004), who reported small *C. ignobilis* in turbid regions of Kaneohe Bay and medium size *C. ignobilis* on inshore reefs within Kaneohe Bay.

Understanding how species move in dynamic environments is essential for assessing the efficacy of management measures. This study showed distinct movement strategies from both species, which suggests effective management strategies will require species-specific approaches. Although both species are targeted regionally by recreational fishers and are important in Indo-Pacific inshore fisheries (Gunn 1990, Grandcourt et al. 2004, DSEWPC 2012), little information is available on their ecology and status. Consequently, it is unknown if these species are vulnerable to fishing and if they benefit from management already in place. This study provides a better understanding of *C. ignobilis* and *G. speciosus* movement patterns and interactions with their environment that may offer some insight on their potential vulnerability to fishing. Gruss et al. (2011) found that populations displaying distinct types of migration, have different levels of vulnerability to fishing and receive variable benefits from marine protected areas. Given their ecological importance, significance for fisheries, and their potential vulnerability to fishing, it is recommended that more research on these species should be undertaken to support well-informed spatial management plans.

Acknowledgements. We thank staff and students at the Centre for Sustainable Tropical Fisheries and Aquaculture, including J. Matley, O. Li, V. Udawyer, M. Espinoza, P. Yates, S. Moore, L. Currey; also M. Green for genetic skills; and M. Kaminski and S. Sutton for their fly fishing skills. We thank the editor and 3 reviewers for helpful comments. Project funding was awarded to M.R.H. and C.A.S. via the National Environmental Research Project. E.J.I.L. was supported by an Australian Postgraduate Award and the College of Marine and Environmental Sciences, James Cook University. All surgical procedures were conducted under Animal Ethics permit A1933 approved by James Cook University. Map data were provided by the Great Barrier Reef Marine Park Authority and Queensland Department of Environment and Resource Management.

LITERATURE CITED

- Allen GL, Yoklavich MM, Cailliet GM, Horn MH (2006) Bays and estuaries. In: Allen LG, Horn MH (eds) Ecology of marine fishes: California and adjacent waters. University of California Press, Berkeley, CA, p 119–148
- Andrews KS, Harvey CJ (2013) Ecosystem-level consequences of movement: seasonal variation in the trophic impact of a top predator. Mar Ecol Prog Ser 473:247–260
- AIMS (Australian Institute of Marine Science) (2015) Table generated 10th March 2015 using Cleveland Bay Weather Station. Australian Institute of Marine Science, Long term Monitoring and Data Centre. <http://data.aims.gov.au/aimsrtds/datatool.xhtml?site=3>
- Barton K (2014) MuMIn: Multi-model inference. R package version 1.10.0. <http://CRAN.R-project.org/package=MuMIn>
- Begg GA, Chen CCM, O'Neil MF, Rose DB (2006) Stock assessment of the Torres Strait Spanish mackerel fishery. CRC Reef Research Centre, Townsville
- Blaber SJM, Cyrus DP (1983) The biology of Carangidae (Teleostei) in natal estuaries. J Fish Biol 22:173–188
- Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MH, White JS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol Evol 24:127–135
- Burnham KP, Anderson DR (2002) Information and likelihood theory: a basis for model selection and inference. In: Burnham K, Anderson D (eds) Model selection and multimodel inference. Springer, New York, NY, p 49–97
- Chapman BB, Hulthen K, Brodersen J, Nilsson PA, Skov C, Hansson LA, Bronmark C (2012) Partial migration in fishes: causes and consequences. J Fish Biol 81:456–478
- Chin A, Heupel MR, Simpfendorfer CA, Tobin AJ (2016) Population organisation in reef sharks: new variations in coastal habitat use by mobile marine predators. Mar Ecol Prog Ser 544:197–211
- Clark BM, Bennett BA, Lamberth SJ (1996) Temporal variations in surf zone fish assemblages from False Bay, South Africa. Mar Ecol Prog Ser 131:35–47
- Croft DP, James R, Krause J (2008) Exploring animal social networks. Princeton University Press, Princeton, NJ
- Croft DP, Madden JR, Franks DW, James R (2011) Hypothesis testing in animal social networks. Trends Ecol Evol 26:502–507
- Csardi G, Nepusz T (2006) The igraph software package for complex network. InterJournal Complex Systems:1695. www.interjournal.org
- Currey LM, Heupel MR, Simpfendorfer CA, Williams AJ (2014) Sedentary or mobile? Variability in space and depth use of an exploited coral reef fish. Mar Biol 161: 2155–2166
- DSEWPC (Australia. Department of Sustainability, Environment, Water, Population and Communities) (2012) Assessment of the East Coast inshore fin fish fishery. DSEWPC, Commonwealth of Australia, Canberra
- Espinoza M, Lédée EJ, Simpfendorfer CA, Tobin AJ, Heupel MR (2015) Contrasting movements and connectivity of reef-associated sharks using acoustic telemetry: implications for management. Ecol Appl 25: 2101–2118
- Finn JT, Brownscombe JW, Haak CR, Cooke SJ, Cormier R, Gagne T, Danylchuk AJ (2014) Applying network methods to acoustic telemetry data: modeling the movements of tropical marine fishes. Ecol Modell 293:139–149

- Fox J, Weisberg S (2011) An R companion to applied regression. Sage, Thousand Oaks, CA. <http://socserv.socsci.mcmaster.ca/jfox/Books/Companion>
- Fruchterman TMJ, Reingold EM (1991) Graph drawing by force-directed placement. *Softw Prac Exper* 21: 1129–1164
- Grandcourt EM, Al Abdessalaam TZ, Francis F, Al Shamsi A (2004) Population biology and assessment of representatives of the Family Carangidae: *Carangoides bajad* and *Gnathanodon speciosus* (Forsskål, 1775), in the Southern Arabian Gulf. *Fish Res* 69:331–341
- Grueber CE, Nakagawa S, Laws RJ, Jamieson IG (2011) Multimodel inference in ecology and evolution: challenges and solutions. *J Evol Biol* 24:699–711
- Gruss A, Kaplan DM, Guenette S, Roberts CM, Botsford LW (2011) Consequences of adult and juvenile movement for marine protected areas. *Biol Conserv* 144:692–702
- Gunn JS (1990) A revision of selected genera of the Family Carangidae (Pisces) from Australian waters, Vol 12. The Australian Museum, Sydney
- Gunn JS, Stevens JD, Davis TLO, Norman BM (1999) Observations on the short-term movements and behaviour of whale sharks (*Rhincodon typus*) at Ningaloo Reef, Western Australia. *Mar Biol* 135:553–559
- Halpern BS, Walbridge S, Selkoe KA, Kappel CV and others (2008) A global map of human impact on marine ecosystems. *Science* 319:948–952
- Heupel MR, Simpfendorfer CA (2014) Importance of environmental and biological drivers in the presence and space use of a reef-associated shark. *Mar Ecol Prog Ser* 496:47–57
- Heupel MR, Simpfendorfer CA, Hueter RE (2004) Estimation of shark home ranges using passive monitoring techniques. *Environ Biol Fishes* 71:135–142
- Heupel MR, Simpfendorfer CA, Collins AB, Tyminski JP (2006) Residency and movement patterns of bonnethead sharks, *Sphyrna tiburo*, in a large Florida estuary. *Environ Biol Fishes* 76:47–67
- Holland KN, Lowe CG, Wetherbee BM (1996) Movements and dispersal patterns of blue trevally (*Caranx melampygus*) in a fisheries conservation zone. *Fish Res* 25: 279–292
- Jacoby DMP, Brooks EJ, Croft DP, Sims DW (2012) Developing a deeper understanding of animal movements and spatial dynamics through novel application of network analyses. *Methods Ecol Evol* 3:574–583
- James NC, Cowley PD, Whitfield AK, Lamberth SJ (2007) Fish communities in temporarily open/closed estuaries from the warm- and cool-temperate regions of South Africa: a review. *Rev Fish Biol Fish* 17:565–580
- Johnson JB, Omland KS (2004) Model selection in ecology and evolution. *Trends Ecol Evol* 19:101–108
- Kininmonth SJ, De'ath G, Possingham HP (2010) Graph theoretic topology of the Great but small Barrier Reef world. *Theor Ecol* 3:75–88
- Knip DM, Heupel MR, Simpfendorfer CA (2010) Sharks in nearshore environments: models, importance, and consequences. *Mar Ecol Prog Ser* 402:1–11
- Knip DM, Heupel MR, Simpfendorfer CA, Tobin AJ, Moloney J (2011) Ontogenetic shifts in movement and habitat use of juvenile pigeye sharks *Carcharhinus amboinensis* in a tropical nearshore region. *Mar Ecol Prog Ser* 425:233–246
- Knip DM, Heupel MR, Simpfendorfer CA (2012a) Evaluating marine protected areas for the conservation of tropical coastal sharks. *Biol Conserv* 148:200–209
- Knip DM, Heupel MR, Simpfendorfer CA (2012b) Habitat use and spatial segregation of adult spottail sharks *Carcharhinus sorrah* in tropical nearshore waters. *J Fish Biol* 80:767–784
- Langton RW, Steneck RS, Gotceitas V, Juanes F, Lawton P (1996) The interface between fisheries research and habitat management. *N Am J Fish Manage* 16:1–7
- Lédée EJI, Heupel MR, Tobin AJ, Knip DM, Simpfendorfer CA (2015a) A comparison between traditional kernel-based methods and network analysis: an example from two nearshore shark species. *Anim Behav* 103:17–28
- Lédée EJI, Heupel MR, Tobin AJ, Simpfendorfer CA (2015b) Movements and space use of giant trevally in coral reef habitats and the importance of environmental drivers. *Anim Biotelem* 3:6
- Matley JK, Heupel MR, Simpfendorfer CA (2015) Depth and space use of leopard coralgrouper *Plectropomus leopardus* using passive acoustic tracking. *Mar Ecol Prog Ser* 521:201–216
- Meyer CG, Holland KN, Wetherbee BM, Lowe CG (2001) Diet, resource partitioning and gear vulnerability of Hawaiian jacks captured in fishing tournaments. *Fish Res* 53:105–113
- Meyer CG, Holland KN, Papastamatiou YP (2007) Seasonal and diel movements of giant trevally *Caranx ignobilis* at remote Hawaiian atolls: implications for the design of Marine Protected Areas. *Mar Ecol Prog Ser* 333:13–25
- Mills EL, Confer JL, Ready RC (1984) Prey selection by young yellow perch: The influence of capture success, visual acuity, and prey choice. *Trans Am Fish Soc* 113: 579–587
- Mourier J, Vercelloni J, Planes S (2012) Evidence of social communities in a spatially structured network of a free-ranging shark species. *Anim Behav* 83:389–401
- Munroe SEM, Simpfendorfer CA, Moloney J, Heupel MR (2015) Nearshore movement ecology of a medium-bodied shark, the creek whaler *Carcharhinus fitzroyensis*. *Anim Biotelem* 3:10
- Nash KL, Welsh JQ, Graham NA, Bellwood DR (2015) Home-range allometry in coral reef fishes: comparison to other vertebrates, methodological issues and management implications. *Oecologia* 177:73–83
- Nemeth RS (2012) Ecosystem aspects of species that aggregate to spawn. In: Sadovy de Mitcheson Y, Colin PL (eds) *Reef fish spawning aggregations: biology, research and management*, Vol 35. Springer Netherlands, Dordrecht, p 21–56
- Persis M, Chandra Sekhar Reddy A, Rao LM, Khedkar GD, Ravinder K, Nasruddin K (2009) COI (cytochrome oxidase-I) sequence based studies of Carangid fishes from Kakinada coast, India. *Mol Biol Rep* 36:1733–1740
- Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2014) nlme: linear and nonlinear mixed effects models. R package version 3.1-117. <http://CRAN.R-project.org/package=nlme>
- Puvanendran V, Brown JA (2002) Foraging, growth and survival of Atlantic cod larvae reared in different light intensities and photoperiods. *Aquaculture* 214:131–151
- R Development Core Team (2014) R: a language and environment for statistical computing, v.3.1.0. R Foundation for Statistical Computing, Vienna. www.R-project.org
- Randall JE, Allen GR, Steene RC (1997) Fishes of the Great Barrier Reef and Coral Sea, rev. edn. University of Hawai'i Press, Honolulu, HI

- Rayfield B, Fortin MJ, Fall A (2011) Connectivity for conservation: a framework to classify network measures. *Ecology* 92:847–858
- Roessig JM, Woodley CM, Cech JJ, Hansen LJ (2004) Effects of global climate change on marine and estuarine fishes and fisheries. *Rev Fish Biol Fish* 14:251–275
- Schielzeth H (2010) Simple means to improve the interpretability of regression coefficients. *Methods Ecol Evol* 1:103–113
- Stehfest KM, Patterson TA, Dagorn L, Holland KN, Itano D, Semmens JM (2013) Network analysis of acoustic tracking data reveals the structure and stability of fish aggregations in the ocean. *Anim Behav* 85:839–848
- Stehfest KM, Patterson TA, Barnett A, Semmens JM (2015) Markov models and network analysis reveal sex-specific differences in the space-use of a coastal apex predator. *Oikos* 124:307–318
- Stoner AW, Manderson JP, Pessutti JP (2001) Spatially explicit analysis of estuarine habitat for juvenile winter flounder: combining generalized additive models and geographic information systems. *Mar Ecol Prog Ser* 213: 253–271
- Sudekum AE, Parrish JD, Radtke RL, Ralston S (1991) Life-history and ecology of large jacks in undisturbed, shallow, oceanic communities. *Fish Bull* 89:493–513
- Taylor S, Webley J, McInnes K (2012) 2010 statewide recreational fishing survey. Fisheries Queensland, Department of Agriculture, Fisheries and Forestry, State of Queensland, Brisbane
- Tobin AJ, Mapleston A, Harry AV, Espinoza M (2014) Big fish in shallow water; use of an intertidal surf-zone habitat by large-bodied teleosts and elasmobranchs in tropical northern Australia. *Environ Biol Fishes* 97: 821–838
- Udyawer V, Chin A, Knip DM, Simpfendorfer CA, Heupel MR (2013) Variable response of coastal sharks to severe tropical storms: environmental cues and changes in space use. *Mar Ecol Prog Ser* 480:171–183
- Urban DL, Keitt T (2001) Landscape connectivity: a graph-theoretic perspective. *Ecology* 82:1205–1218
- West DB (2001) Introduction to graph theory, Vol 2. Prentice Hall, London
- Wetherbee BM, Holland KN, Meyer CG, Lowe CG (2004) Use of a marine reserve in Kaneohe Bay, Hawaii by the Giant trevally, *Caranx ignobilis*. *Fish Res* 67:253–263
- Wilson ADM, Krause S, Ramnarine IW, Borner KK, Clément RJC, Kurvers RHJM, Krause J (2015) Social networks in changing environments. *Behav Ecol Sociobiol* 69: 1617–1629
- Wittemyer G, Douglas-Hamilton I, Getz WM (2005) The socioecology of elephants: analysis of the processes creating multitiered social structures. *Anim Behav* 69: 1357–1371
- Zar JH (1999) Biostatistical analysis, 4th edn. Simon & Schuster, Upper Saddle River, NJ
- Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. *Methods Ecol Evol* 1:3–14

Editorial responsibility: Janet Ley,
St. Petersburg, Florida, USA

Submitted: November 20, 2015; *Accepted:* May 17, 2016
Proofs received from author(s): June 23, 2016