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Influence of tidally induced fronts and Langmuir circulations on distribution and movements of presettlement fishes around a coral reef

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Abstract. The slicks of tidally induced fronts and Langmuir circulations were studied near Bowden Reef, Great Barrier Reef, in December 1987. There were two components to the study: (1) a description of physical oceanography adjacent to the reef; (2) sampling for planktonic organisms, designs being stratified according to hydrology. Tidal fronts extended 1 to 2 km from the reef outside the lagoon. Fish of a variety of developmental forms and zooplankton were most abundant in slicks of fronts. Sixteen to 81% of fish that were captured were presettlement reef-fishes. There was an unclear relationship between the presence of slicks of Langmuir circulations and abundance of fish in the lagoon. This relationship was largely because well developed atherinids and recently hatched pomacentrids showed no predictable relationship with the presence of windrows. Jellyfish, *Aurelia aurita*, were found in extremely high concentrations in the slicks of Langmuir circulations; small carangids were associated with jellyfish. Movements of fronts were influenced by the tide and wind. In some conditions we observed fronts to change position as the tide reversed direction. Fronts that were orientated offshore (1 to 2 km), were observed to rotate and align with the reef. Because of a "halo" of oceanographic features such as tidal fronts, the reef may be a larger target for presettlement fishes than its topography would suggest. It is argued that some organisms are advected into slicks, while others respond to high concentrations of zooplanktonic food and remain in slicks. Localised oceanographic features may also affect the settlement patterns of fishes on reefs.

Introduction

The Great Barrier Reef (GBR) is composed of many individual reef systems. The reproductive products of fish associated with reefs are released into the plankton as eggs or free-swimming fishes. It is, therefore, unlikely that reefs are reproductively closed systems (Sale 1980). The distribution patterns and residence times of presettlement fish adjacent to reefs may be modified by the dynamics of water circulation, as may the settlement patterns of fish on reefs.

There is a substantial body of information on the adult and juvenile phases of reef fishes (Sale 1980, Doherty and Williams 1988). By comparison, little is known of the presettlement phase. Information on the distribution of the presettlement phase of fishes on the GBR is of four general forms. (1) Coarse-scale patterns (1 to 100 km) of abundance across the "Great Barrier Reef lagoon" (Leis and Goldman 1984, 1987, Leis 1986, Milward and Hartwick 1986, Williams et al. 1988). (2) Abundance of presettlement fishes on windward and leeward sides of Lizard Island (Leis 1986, Doherty 1987) and in a closed lagoon (Leis 1981, Schmitt 1986). (3) Modelling trajectories of presettlement fish as passive neutrally buoyant particles according to mean flow (Williams et al. 1984, Dight et al. 1989). (4) Use of patterns of recruitment to speculate on the distribution of presettlement fishes in terms of patch size. For example, patch sizes of up to 100 km have been estimated (Doherty 1987). Only Categories 1 and 2 involve the direct sampling of presettlement fishes. Clearly more information is required on the distribution and movements of presettlement fishes, near to and away from reefs.

Localised oceanographic features in shelf waters have an important influence on the distribution of presettlement fishes and zooplankters (Alldredge and Hamner 1980, Owen 1981, Le Fèvre 1986, Oliver and Willis 1987). Furthermore, oceanographic structure such as the slicks of internal waves and Langmuir circulations not only influence distribution patterns of fishes and zooplankton, but may influence their direction of movement (Shanks 1983, 1986, Hamner and Schneider 1986, Kingsford and Choat 1986, Kingsford 1990). Of particular interest for meroplankton is onshore transport to the reef. A number of potentially important hydrological features are found close to reefs. These include tidally generated eddies, jets, fronts, thermal plumes and, in windy conditions over 10 knots, Langmuir circulations (Alldredge and Hamner 1980, Wolanski et al. 1984, 1989, Sakamoto and Tanaka

1986, Wolanski 1986, Wolanski and Hamner 1988). All these features are potentially important to influence aggregation, to entrain or retain organisms near reefs, to concentrate planktonic food, and to act as oceanographic cues for the presence of reefs.

Our specific aims were to: (1) describe tidal flow and the dynamics of tidal fronts close to the reef; (2) sample presettlement fishes and zooplankton associated with fronts near the reef; (3) study waters of the reef lagoon by using sampling that was stratified according to hydrology and by sampling at fixed locations in the lagoon. The last aim focused primarily on the slicks of Langmuir circulations (windrows). We argue that an evaluation of the role of surface oceanographic features in modifying distributions of presettlement fish is a prerequisite for understanding the process of settlement in reef fishes.

Materials and methods

Study area and physical oceanography

The study was carried out in December 1987 at Bowden Reef on the Central Great Barrier Reef (Fig. 1 A). Current meters were deployed at Sites A, F, G, H, I, J, C and D near the surface, on a transect across Bowden Reef Lagoon (Fig. 1 B, C). In Deep-Water Sites A, F, G, C, D and E, a current meter was deployed at mid-

Table 1. Designs used to sample presettlement fishes in vicinity of Bowden Reef, December 1987. Design a was completed twice: Locations 1–5 = Time 1; Locations 6–10 = Time 2; Slick: convergence of oceanographic feature; ripple: rippled water adjacent to slick. Formal analyses (ANOVA) were performed for Design a only; hydrology was treated as a fixed factor and location as a random factor

Factor	Treatments
Design a: tidal fronts (within 2 km of Bowden Reef)	
Hydrology	slick ripple
Location	1–5
Replicates	$n=3$
Design b: Langmuir circulations (within lagoon)	
Hydrology	slick ripple
Location	1–5
Replicates	$n=3$
Design c: fixed sites within lagoon	
Time	1–3
Sites	1–3
Replicates	$n=3$

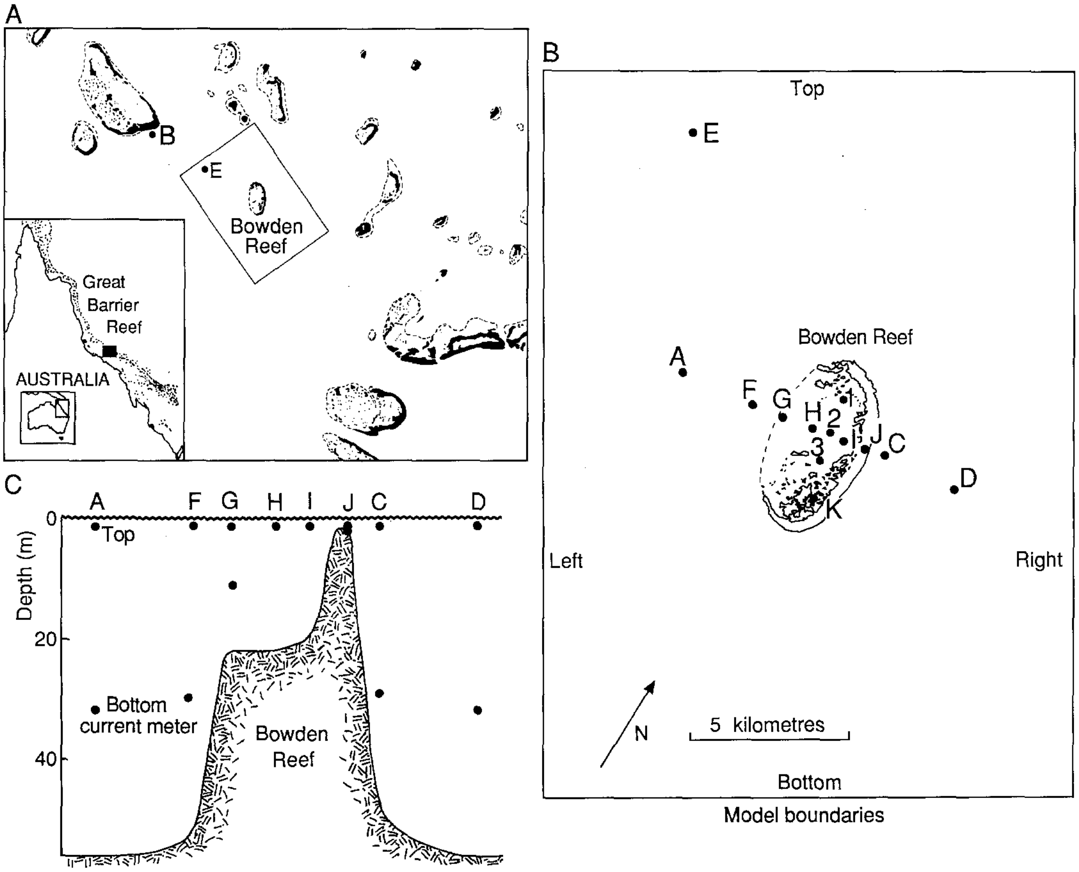

Fig. 1. Study area. (A) Location of Bowden Reef, Central Great Barrier Reef; current meters were deployed at Sites B and E. (B) Detailed map of reef showing location of positions on Transect A–D and among coral outcrops (K) in which current meters were deployed. Sites 1–3 were sampled in Sampling Design "c" (Table 1). (C) Vertical relief of reef showing position along transect of bottom current-meters and those near surface

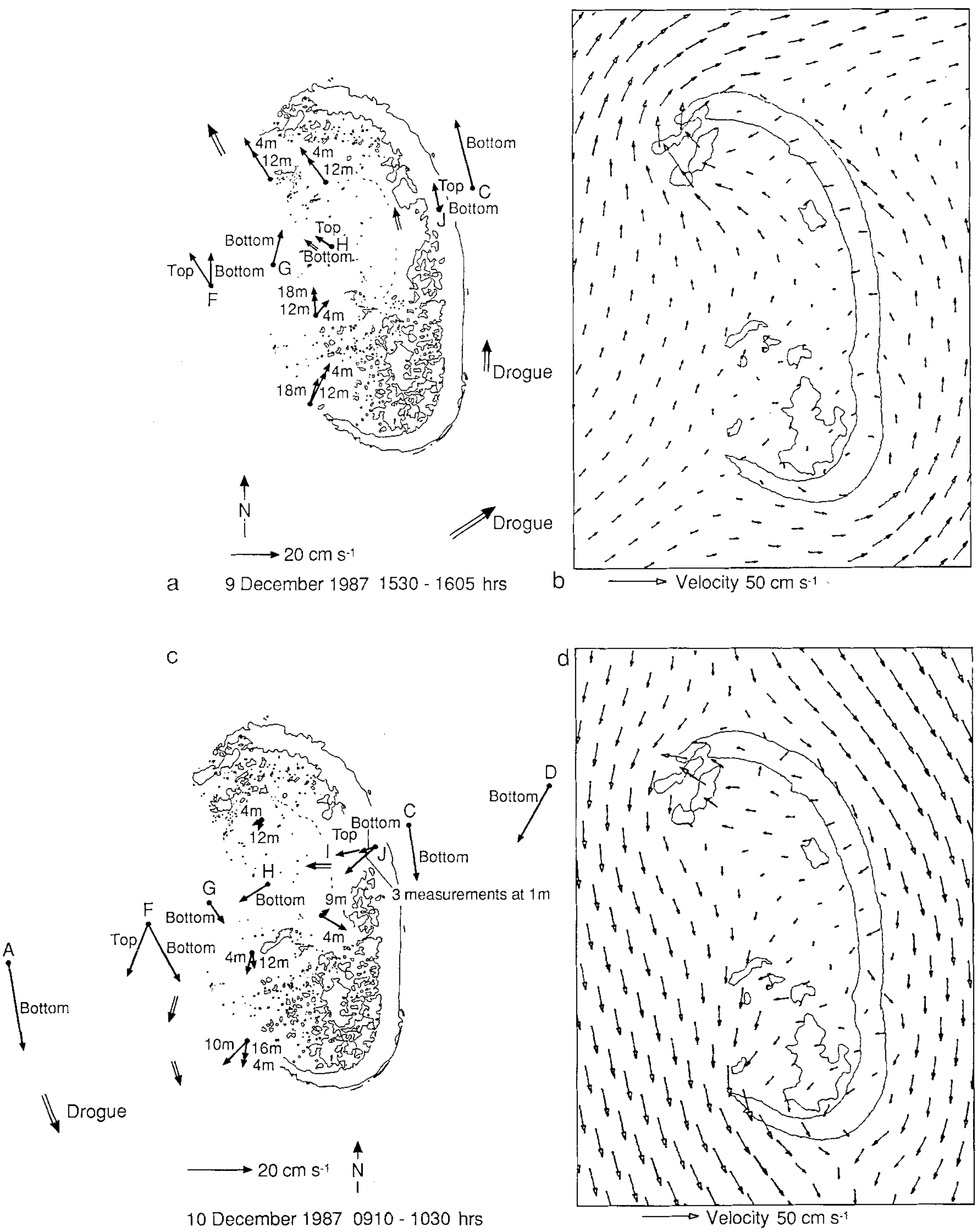

Fig. 2. Typical drogue trajectories from different positions around Bowden Reef (a, c) and predicted synoptic distribution of currents on 9 December 1987 ebb tide (b) and 10 December 1987 flood tide (d). Arrows show current directions

depth. The meter was either an Inter-Ocean Model S4 meter or an Aanderaa RCM4-S meter. At Site B, two meters were deployed, one at mid-depth and one near the surface. In addition, an S4 current meter was deployed at 1.5 m depth under a 2 m-long rod held at the surface by buoys, at Sites A, F, and C. In the lagoon, S4 meters were deployed 2 m below the surface at Sites H and I throughout the experiment, and at Site K (in a maze of coral outcrops) only for one day at the end of the experiment. At Site J, over the reef flat, two S4 meters were held one above the other in a bottom-mounted aluminium frame. The meters were located at 0.4 and 1.3 m above the bottom. The top meter surfaced during low spring tides.

Aanderaa Model WL5 bottom-mounted tide gauges were deployed, attached to railway wheels or concrete blocks on the bottom, at Sites A and J. A meteorological buoy, that included wind speed and direction sensors 2.5 m above the sea level, was moored in the lagoon halfway between Sites H and I. All the meteorological and oceanographic instruments provided data at 10 min intervals. Radar-tracked drogues with 2×2 m sub-surface sails, were deployed on occasions. The depth of the sails was either 2 or 10 m below the surface, according to whether they were in the lagoon or in deep water. On occasion, the three-dimensional water circulation was measured by anchoring a small boat over the lagoon at various

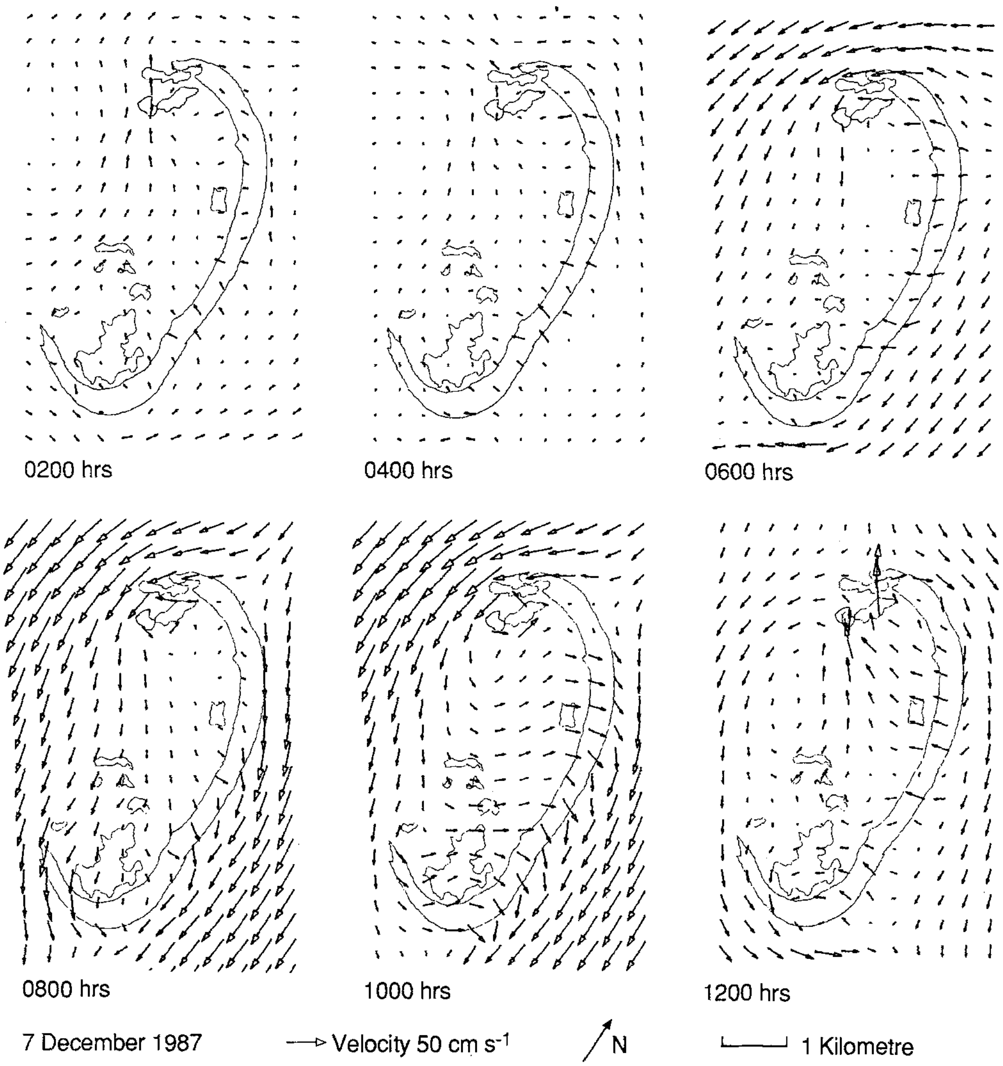

Fig. 3. Synoptic views of depth-averaged predicted currents at 2 h intervals during spring tides

sites. The S4 current meter was suspended from the boat, and current was recorded at a given depth for 1 min. The current meter was lowered a fixed increment of 0.5 m and the procedure of current measurement was repeated until the meter reached the bottom. Vertical profiles of salinity and temperature were occasionally collected using an Australian Institute of Marine Science CTD profiler (accuracy <0.01 ‰ and C°).

A total of 80 kg of PVC neutrally-buoyant beads, with a nominal diameter of 0.5 mm, were released uniformly along a straight line between Sites K and I, between 05:45 and 06:45 hrs on 11 December 1987. Some beads were later recovered in plankton trawls sampling for coral planulae and presettlement fishes.

Sampling with purse-seine net

All the biological samples were taken using a plankton-mesh purse-seine net. The net was identical to that described by Kingsford and Choat (1985), except that the length of the net was increased to 14 m. A mesh size of 0.28 mm was appropriate to catch reef fishes that were of sizes and developmental forms ranging from newly hatched individuals to juveniles (Leis and Rennis 1983). The estimated volume of water sampled by the net was 31 m^3. All samples were preserved in 2 to 5% formalin to reduce the shrinkage of specimens. The net was rinsed in the ocean two to four times after each seine, and the contents of the rinse were saved in the sample jar also. Total counts of fish were made for each sample.

Sampling procedure and design

Most of the sampling was done in and out of slicks from a 3 m Zodiac inflatable boat. Water that was sampled adjacent to slicks was rippled. Three designs were used in the study (Table 1). Slicks of tidal fronts were sampled within 2 km of the reef, but never within the lagoon. Slicks were visible only when winds were below the range of 7 m s^{-1}. We searched for slicks by motoring in a zig-zag pattern, perpendicular to the north-south axis of the reef. The position of some slicks was predicted based upon the state of the tide. The exact position of the inflatable in relation to Bowden Reef was determined by radar from the support vessel R. V. "Lady Basten." The sampling design was completed twice on 7–8 December and 13–14 December 1987, corresponding to periods before and after a windy spell.

The slicks of Langmuir circulations (i.e., windrows) were sampled in the lagoon of Bowden Reef (Design b in Table 1). Winds were in excess of 7 m s^{-1} and slicks were visible as illustrated by Faller and Woodcock (1964) and Faller and Auer (1988). The slicks of windrows were always more diffuse than those of tidal fronts. Sampling was between 10 and 12 December.

When no slicks were observed in the lagoon sampling was done at three sites; 1, 2 and 3 (Design c; Fig 1 B, Table 1). Sites were identified by anchored buoys or structural features of the lagoon. The design was repeated on three occasions to determine how presettlement fishes were distributed in the lagoon in the absence of obvious hydrological features. Sampling was between 6 and 10

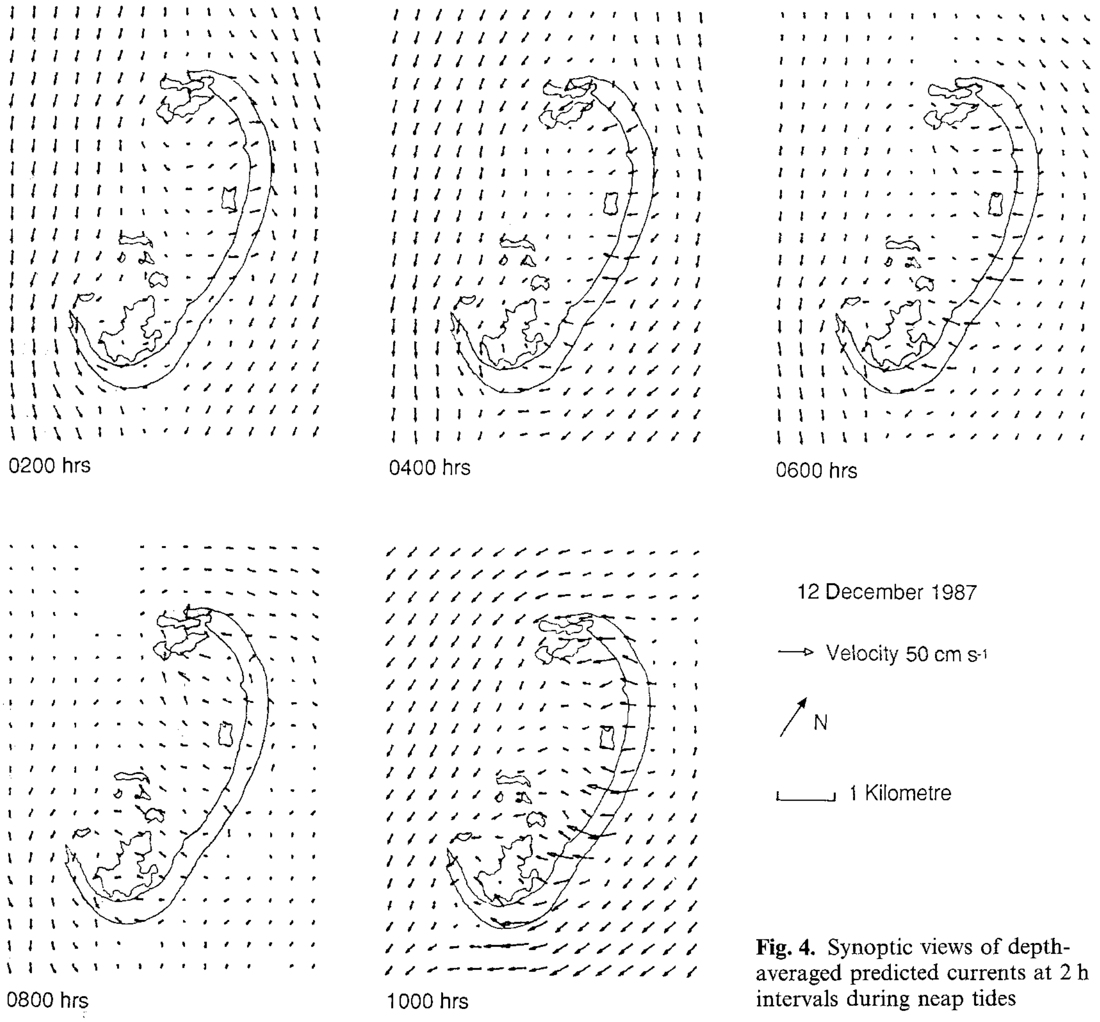

Fig. 4. Synoptic views of depth-averaged predicted currents at 2 h intervals during neap tides

December. Where appropriate, data were analysed using analysis of variance according to the recommendations of Underwood (1981). Homogeneity of the data was tested using Cochran's test. Where the test was significant, the data were transformed and reanalysed for heteroscidacity.

Terminology

The presettlement phase of reef fishes refers to the period from egg hatching to settlement on a reef. This period of the life history of the reef fishes was not called the larval phase because many fish spend some time in the pelagic environment as juveniles; this issue has been discussed in detail by Kingsford (1988). Some of the fishes captured in this study were reef-associated planktivores (e.g., Atherinidae), for these groups the end of the presettlement phase refers to their association with the reef as juveniles. The term "pelagic fish" refers to fish that spend their entire life history in the pelagic environment. Developmental forms are named according to Leis and Rennis (1983); for example, flexion and postflexion fish. The standard lengths of fish were measured or, in the case of very small fish, notochord length.

Results

Physical oceanography

The tide was semi-diurnal with strong diurnal inequality; neap tides of 0.5 m prevailed on 12 to 15 December, and spring tides of 3 m amplitude on 3 to 7 December. The difference in tidal elevations between Site J and Site A was always less than 2 cm. The wind was consistently to the west, with deviations of only ± 30°, and a magnitude of typically 5 to 15 $\mathrm{m\ s^{-1}}$.

The prevailing longshore current was southward. In offshore waters (i.e., offshore from the reef) the current changed from $<0.02\ \mathrm{m\ s^{-1}}$ at spring tide to $\sim 0.10\ \mathrm{m}^{-1}$ at neap tide. Wolanski et al. (1989) observed this phenomenon a year later, in November 1988, when northerly winds prevailed. This change of the longshore current in offshore waters is thus probably not wind-driven, but may instead be attributable to a non-linear friction-driven interaction between tidal and low-frequency currents (Provis and Lennon 1983, Wolanski and Thompson 1984, Wolanski et al. 1988, 1989).

Currents around the reef and in the lagoon reversed at times (Fig. 2). The wind has a dominant influence on lagoon circulation. Indeed in November 1986, a wind prevailed from the north and resulted in a strong ($\sim 0.1\ \mathrm{m\ s^{-1}}$) southward current in the lagoon at neap tide (Wolanski et al. 1989). In December 1987, on the other hand, when a wind prevailed to the west, the currents in the lagoon at Site 1 varied from westward to northward.

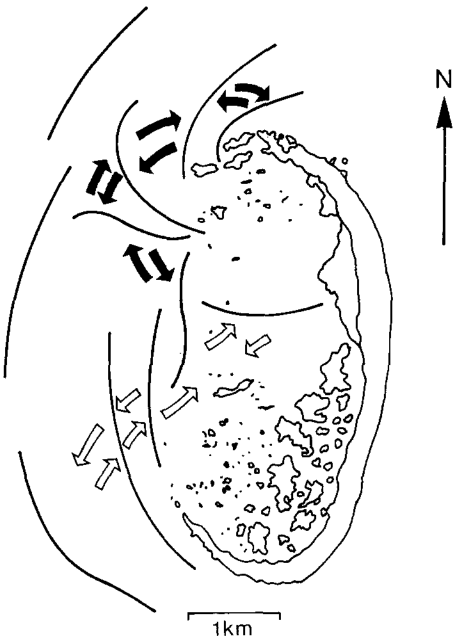

Fig. 5. Slicks sampled for biological component of study (excluding slick in middle of lagoon). Note topographically controlled front off north-west corner of reef which rotated to north or south according to state of tide (pooled observations over entire study period). Filled arrows show observed directions of the movements of slicks, which changed according to state of tide; on spring tides, slicks were advected into lagoon. Hollow arrows indicate predicted movements of slicks

Typical synoptic views of observed currents, in both offshore and lagoon waters, are shown in Fig. 2. Prevailing offshore elements were weaker than the reversing tidal current, the flood tidal current flowing southward around Bowden Reef, and the ebb tidal current flowing northward. The drogue and current-meter data allowed us to fine-tune the numerical model of the depth-averaged water circulation around Bowden Reef described by Wolanski et al. (1989).

Synoptic views of depth-averaged predicted currents are shown at two-hourly intervals in Figs. 3 and 4 for spring and neap tides, respectively. There were complex recirculating flows on the northeastern side of Bowden Reef; these were particularly prevalent when the longshore current was slowest. When a strong onshore current prevailed, these eddies were short-lived and a through-reef-lagoon net-current resulted that completely flushed out the lagoon in 1 to 2 d.

More importantly, an examination of these data suggests the presence of a tidally-driven topographically-controlled anti-clockwise-rotating baratropic front (extending from the surface to the substratum) on the western side of Bowden Reef. Slicks of this front were observed off the north-west side of the reef and swung to north or south depending on phase of the tide (Fig. 5). This front would form initially at the boundary of eddies and along shear layers. Such eddies aggregate water-borne particles along baratropic fronts, since the lagoon waters are shallow enough for bottom friction to generate a strong three-dimensional internal circulation (Wolanski and Hamner 1988, Deleersnijde et al. 1989). This front was highly visible as a slick and accompanied by the presence of aggregations of jellyfish and other plankton. The front was purely barotropic, i.e., driven by current shear and bottom friction, as differences in salinity and temperature across the front were too small to measure (<0.0‰ S and <0.1 °C). That these fronts aggregated particles originating from the lagoon was made apparent by the recovery of PVC beads in plankton tows within the front, but not elsewhere in the lagoon. Evidence for aggregation of organisms outside the lagoon is presented in the following subsection.

Fronts that extended past the reef were often characterised by an abundance of the blue-green alga, *Oscillatoria erthraeus*. From observations over the entire study period on the north-west tip of the reef, the frontal system typically swung from the north-west to the south-west according to state of the tide (Fig. 5). This structure often extended over 1 km from the reef during changes of the tide. In some cases parts of the front drifted over the lagoon or toward the reef on the northern side. Accordingly, the front dynamics swept free-floating organisms

Table 3. Analyses of variance for four categories of fishes in slicks of tidal fronts and in adjacent water, on two occasions (combined data) DF: degrees of freedom for *F*-test, MS: mean square; *P*: probability level. Cochran's *C*-tests were used to test homogeneity of variance (20 variances, 2 DF); brackets denote a nested term

Source of variation	DF	MS	*F*	*P*
Reef fishes, $C=0.27$, NS; data were untransformed				
Time, T	1,8	173.4	1.2	NS
Hydrology, H	1,8	1025.1	6.5	<0.05
T×H	1,8	153.6	1.0	NS
Location [T]	8,40	145.1	4.0	<0.005
H×L (T)	8,40	158.1	4.3	<0.001
Residual	40	36.6		
Pelagic fishes, $C=0.21$, NS; data were log $(x+1)$ transformed				
Time, T	1,8	2.04	0.28	NS
Hydrology, H	1,8	45.3	6.12	<0.05
T×H	1,8	2.68	0.36	NS
Location [T]	8,40	7.3	12.1	<0.001
H×L (T)	8,40	7.4	12.2	<0.001
Residual	40	0.6		
Preflexion and flexion-stage fishes, $C=0.25$ NS; data were log $(x+1)$ transformed				
Time, T	1,8	1.13	0.76	NS
Hydrology, H	1,8	5.37	3.09	NS
T×H	1,8	2.3	1.34	NS
Location [T]	8,40	1.5	3.18	<0.01
H×L (T)	8,40	1.7	3.73	<0.005
Residual	40	0.5		
Postflexion and pelagic juvenile fishes, $C=0.26$; data were log $(x+1)$ transformed				
Time, T	1,8	4.89	2.4	NS
Hydrology, H	1,8	18.16	9.51	<0.05
T×H	1,8	0.9	0.48	NS
Location [T]	8,40	2.04	5.15	<0.001
H×L (T)	8,40	1.9	4.82	<0.001
Residual	40	0.4		

Table 2. Density [mean nos. 31 m^{-3} (SE); $n=3$ seines] of presettlement and small pelagic fishes in slicks (S) of tidal fronts and adjacent rippled water (R) at ten random locations (Locations 1–5: Time 1, 7–8 December 1987; Locations 6–10: Time 2, 13–14 December 1987. Totals include rare fishes not listed in table (≤2 fish per family caught)

Family	Location 1		Location 2		Location 3		Location 4		Location 5	
	S	R	S	R	S	R	S	R	S	R
Reef fishes										
Atherinidae	1.3 (0.9)	0	0.3 (0.3)	0.3 (0.3)	0.7 (0.7)	0.3 (0.3)	0	0.7 (0.7)	0	0
Hemiramphidae	1.3 (0.7)	0	0.3 (0.3)	0	0	0	0.3 (0.3)	0	0	0
Dactylopteridae	1.3 (0.7)	0	0	0	0	0	0.3 (0.3)	0	0	0
Mullidae	8.7 (5.2)	0.3 (0.3)	0.3 (0.3)	0	0.3 (0.3)	0	0.7 (0.7)	0.7 (0.7)	0	0
Blenniidae	3.0 (3.0)	0	0	0.3 (0.3)	0	0	0	0	0	0
Apogonidae	0	0	0.7 (0.3)	0	0	0	0.3 (0.3)	0	0	0
Pomacentridae	1.0 (0)	0	2.3 (2.3)	1.0 (0.6)	0	0.7 (0.7)	0.3 (0.3)	0.3 (0.3)	0.7 (0.7)	0
Monacanthidae	0	0	4.0 (2.6)	0	0	0	1.0 (0.6)	0	0	0
Total reef fishes	17.7 (8.2)	1.3 (0.9)	8.3 (5.4)	1.7 (1.2)	1.0 (0.6)	1.0 (0.6)	3.0 (1.7)	1.7 (0.9)	0.7 (0.7)	0
Pelagic fishes										
Spratelloidini	52.0 (36.2)	0	2.0 (1.3)	1.7 (1.7)	0	0	0	0	0.3 (0.3)	0.3 (0.3)
Exocoetidae	14.0 (2.3)	0.7 (0.3)	3.7 (1.3)	0	3.0 (2.1)	0	0	0	0	0
Belonidae	0.3 (0.3)	0	0	0	1.3 (0.9)	0	6.3 (3.0)	0	0	0
Nomeidae	0	0	0	0	1.0 (1.0)	0	0.7 (0.3)	0	0	0
Other Carangidae	0	0	0	0	0	0	0	0	0	0
Seriolina	0.7 (0.3)	0	0	0	0	0	0	0	0	0
Scombroides	0.7 (0.7)	0	0.7 (0.7)	0	0	0	0	0	0	0
Trachinotus	0.3 (0.3)	0	0	0	0	0	0.7 (0.7)	0	0	0
Sphyraenidae	1.0 (1.0)	0	0.3 (0.3)	0	0	0	1.0 (0.6)	0	0	0
Total pelagic fishes	68.7 (34.7)	0.7 (0.3)	6.0 (2.9)	1.7 (1.7)	5.3 (3.9)	0	10.7 (1.7)	0	0.3 (0.3)	0.3 (0.3)
Unknown	0.3 (0.3)	0.3 (0.3)	0	0	0	0	0	0	0	0
Total fishes	86.4 (42.5)	2.0 (1.0)	14.3 (7.9)	3.4 (2.9)	6.3 (3.5)	1.0 (0.6)	13.7 (0.9)	1.7 (0.9)	1.0 (1.0)	0.3 (0.3)

Table 2 (continued)

Family	Location 6		Location 7		Location 8		Location 9		Location 10	
	S	R	S	R	S	R	S	R	S	R
Reef fishes										
Atherinidae	1.7 (0.7)	0	1.0 (1.0)	0	0	0	0	0	1.3 (0.3)	0
Hemiramphidae	0	0	0	0	0	0	0	0	0.3 (0.3)	0
Dactylopteridae	2.0 (1.2)	0	0	0	0.3 (0.3)	0	0.7 (0.7)	1.0 (1.0)	2.3 (0.3)	0.3 (0.3)
Mullidae	2.3 (1.3)	1.0 (0)	1.3 (0.9)	0.3 (0.3)	0	0.3 (0.3)	0.3 (0.3)	0	5.6 (1.5)	0
Blenniidae	3.3 (2.4)	0	3.7 (2.2)	0.3 (0.3)	0.3 (0.3)	0	0.5 (0.3)	0	0.7 (0.7)	0
Apogonidae	0	0	0	0	0	0	0	0.3 (0.3)	0	0
Pomacentridae	3.2 (0.9)	0.3 (0.3)	0.3 (0.3)	0.3 (0.3)	9.0 (4.5)	0	0.3 (0.3)	1.3 (0.9)	5.7 (1.9)	0
Monacanthidae	0	0	0	0	3.0 (1.7)	0.3 (0.3)	6.3 (5.4)	0.7 (0.3)	9.0 (5.7)	0
Total reef fishes	13.0 (5.5)	1.3 (0.3)	6.3 (2.3)	1.0 (0.6)	13.0 (5.5)	0.7 (0.3)	8.7 (4.2)	3.3 (1.2)	25.0 (7.6)	0.3 (0.3)
Pelagic fishes										
Spratelloidini	3.3 (2.9)	4.7 (4.7)	0.3 (0.3)	0	0	0	0.7 (0.7)	0	16.0 (12.5)	0
Exocoetidae	0.7 (0.7)	0	1.3 (0.9)	0	0.3 (0.3)	0	0.3 (0.3)	0	2.3 (0.3)	0
Belonidae	0	0	2.0 (2.0)	0	0.7 (0.3)	0	0.3 (0.3)	0	0.3 (0.3)	0
Nomeidae	0	0	0	0	0	0	0	0	0	0
Other Carangidae	0	0	0	0	0	0	0	1.0 (0.6)	0	0
Seriolina	0	0	0	0	0	0	0	0	0.3 (0.3)	0
Scombroides	0	0	0.3 (0.3)	0	0	0	0	0	3.0 (1.7)	0
Trachinotus	0	0	0	0	0	0	0	0	0	0
Sphyraenidae	0	0	0	0	0	0	0	0	0	0
Total pelagic fishes	4.0 (2.6)	4.7 (4.7)	4.0 (2.6)	0	1.0 (0.6)	0	1.3 (0.7)	1.0 (0.6)	22.3 (13.4)	0
Unknown	0	0	0	0	0	0	0.3 (0.3)	0	0	0
Total fishes	16.0 (8.2)	6.0 (5.0)	10.3 (4.9)	1.0 (0.6)	14.0 (5.0)	0.7 (0.3)	10.3 (3.4)	4.3 (1.5)	47.3 (20.8)	0.3 (0.3)

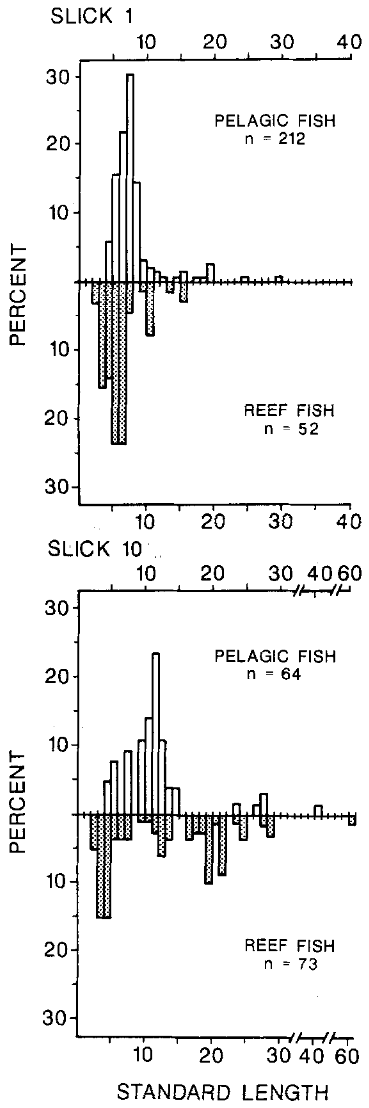

Fig. 6. Sizes (1 mm size classes) of small reef and pelagic fishes captured in slicks at two locations containing high numbers of fish. Ordinates show percentage of each size category, comprised of fishes shown in Table 2

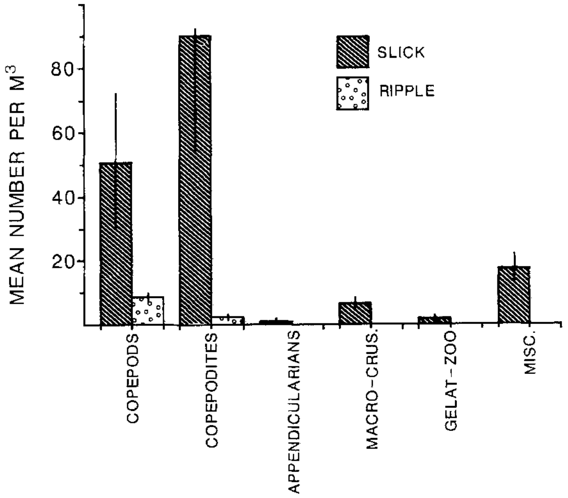

Fig. 8. Abundance of zooplankton (mean ± SE; $n = 3$ seines) in slick of a tidal front and in adjacent rippled water

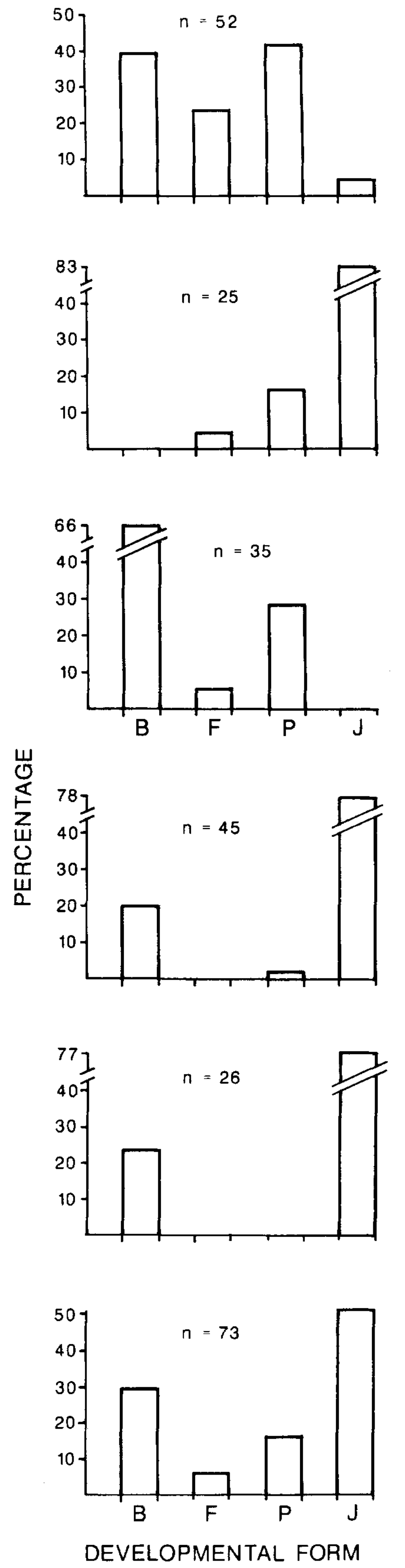

Fig. 7. Developmental forms of fishes from slicks of tidal fronts. Data are presented only for slicks where form of 25 or more fishes was determined (B: preflexion, F: flexion, P: postflexion, J: juveniles). Slicks 1, 2, 6, 8, 9, 10, in order top to bottom). Ordinates show percentage of each form, comprised of fishes shown in Table 2

toward the reef. It is unlikely that long-term trapping of passive particles occurred within the lagoon, because at neap tides a strong through-reef lagoon current prevailed, and at spring tides these fronts and their aggregated material were swept away from the reef with tidal frequency. Potentially, presettlement fish and other organisms could leave the front while it was close to the reef.

Biology of tidal fronts <2 km from reef

The slicks of five tidal fronts were sampled on each of two occasions on the western side of Bowden Reef (7–8 and 13–14 December 1987); these included fronts that swung from the north-west tip of the reef (Fig. 5). Few reef fish were found at some of the ten locations but, where they were abundant, highest concentrations were found in slicks (Table 2). Significant interactions between hydrology and location for pelagic and reef-associated fishes emphasized the variable relationship in concentrations of fishes between slick and rippled areas at different locations (Table 3).

The taxonomic composition of fishes varied between locations (Table 2). For example, at Location 1 no monacanthids were captured while at Location 10 a mean of 9 monacanthids were caught per seine. Fishes of all types were consistently most abundant in slicks. Reef fish that were captured included members of the Atherinidae, Hemiramphidae, Dactyopteridae, Mullidae, Blenniidae, Apogonidae, Pomacentridae and Monacanthidae. The variation in numbers of fishes captured from slicks at different locations could not be explained by the quantity of blue-green algae [volume of *Oscillatoria erthraeus* (ml)] in slicks for reef fish (correlation coefficient, $r=0.2$, DF = 28, NS), pelagic fish ($r=0.2$, DF = 28, NS), preflexion and flexion fish ($r=0.29$, DF = 28, NS) or post-flexion and juvenile fish ($r=0.08$, DF = 28, NS).

Some groups of fish were rare (≤ 2 individuals) and are not listed in Table 2; these were reef fish: Syngnathidae, Ptereleoridae, Tetradontidae, Ostraciidae, Serranidae, Diodontidae, Kyphosidae, Teraponidae, Chaetodontidae and pelagic fish: Myctophidae.

Fishes of a range of sizes were caught, from very small preflexion individuals to juveniles. The size range of fishes varied between slicks (Fig. 6). For example, more large fishes were captured in Slick 10 than in Slick 1. Reef fishes ranged in size from 2 to 60 mm standard length (SL).

The size of a fish does not indicate its developmental form, because representatives of many fish families were caught. The developmental forms of reef fishes were determined from the ten locations. Of 324 fish, 35% were preflexion, 5% flexion, 24% postflexion, and 36% were juveniles. Thus, fishes of all developmental forms were captured during the study. Fishes of all stages were most abundant in slicks; significant effects of hydrology or hydrology × location interactions were detected for early and late developmental forms (Table 3). Depending on the slick that was sampled, however, the proportions of each developmental form varied (Fig. 7). Some slicks had a high percentage of very early developmental forms [preflexion (B) and flexion (F)] and others contained up to 77% juveniles. Clearly, the movement of slicks (which contain large numbers of presettlement juveniles) that transport fishes close to a reef may constitute an important settlement event. Few fishes were captured in rippled water, the developmental form of those that could be determined was as follows: preflexion 60%, postflexion 24%, flexion 0%, juveniles 8.9% (total $n=35$).

An examination of the zooplankton indicated that it was most abundant in slicks, and for many categories concentrations were 4 to 10 times greater in slicks than in rippled areas (Fig. 8). Plankton of a wide range of sizes was most abundant in slicks. For example, very small copepodites (<0.5 mm long), copepods (1 to 2 mm) and large crustaceans, especially shrimps (4 to 6 mm). The miscellaneous category included large numbers of gastropod larvae. A detailed examination of the relationships between fish and plankton is in preparation (Kingsford).

Biology of Langmuir circulations in lagoon

No consistent differences in the abundance of fishes were found between the slicks of windrows and adjacent rippled water in the lagoon; this was true for total fish and reef fishes (Table 4). At some locations fish were most abundant in slicks (e.g. Location 2) and at others in rippled areas (e.g. Location 4). Fishes with distributions that did not relate predictably to slicks or rippled water were *Hypoatherina* sp. (Atherinidae) and pomacentrids (Table 4). Standard errors of 90 to 100% of the mean ($n=3$ seines) generated intractably heterogeneous variances for analyses.

Atherinids were captured in large aggregations both in slicks and rippled water; most of the fish in these aggregations were 12 to 24 mm long (SL). Pomacentrids showed a similar pattern, but consisted of newly hatched individuals. Their distribution appeared to owe more to the location of adult spawning sites than to the physical oceanography of the area. Carangids were also, captured and all were seined in the slicks of windrows (Table 4); these included members of the genus *Carangoides*. Because of high variances these data should be treated with caution. However in the lagoon, fishes appeared to respond or were affected by Langmuir circulations in different ways, depending on their taxonomic group and ontogenetic form. Rare fish (= <2 individuals) included: Mullidae, Exocoetidae and Nomeidae.

The leptomedusa *Aurelia aurita* was found in extremely high concentrations in the lagoon. Abundance was always highest in the slicks of windrows (Fig. 9). The highest density measured in a single seine was 894 *A. aurita* 31 m^{-3}. Most of the carangid fish captured were found in slicks that contained high numbers of *A. aurita*. Although there was no significant relationship between numbers of *A. aurita* and numbers of carangids in slicks ($r=0.02$, DF = 13, NS), a mean (±SE) of 246±146 *A. aurita* ($n=6$ seines) were found in slicks with carangids present and 32±15 *Aurelia* ($n=9$ seines) in slicks from

Table 4. Density [mean nos. 31 m^{-3} (SE); $n = 3$ seines] of presettlement and small pelagic fishes in slicks (S) of Langmuir circulations and adjacent rippled water (R) in lagoon at Bowden Reef. Sampling at five random locations. Totals include rare fishes not listed in table (≤2 fish per family caught)

Family	Location 1		Location 2		Location 3		Location 4		Location 5	
	S	R	S	R	S	R	S	R	S	R
Reef fishes										
Atherinidae	5.0 (5.0)	1.3 (0.9)	0	0	0	0	0	0.7 (0.3)	0.3 (0.3)	11.3 (10.9)
Dactylopteridae	0.7 (0.7)	0.3 (0.3)	0	0	0	0	0	0	0	0
Blenniidae	0	2.7 (1.2)	0	0	0	0	0	0	0	0
Apogonidae	0	0	0	0	0	0	0	4.7 (4.7)	0	0
Pomacentridae	0.3 (0.3)	0.3 (0.3)	0	0	0	3.0 (3.0)	0.3 (0.3)	26.7 (26.7)	0.3 (0.3)	14.3 (13.4)
Total reef fishes	6.3 (5.8)	4.7 (0.3)	0	0	1.3 (0.9)	3.0 (3.0)	0.3 (0.3)	32.0 (24.8)	0.7 (0.7)	25.7 (11.6)
Pelagic fishes										
Spratelloidine	0	0	0	0	0	0	7.0 (7.0)	0	0	0
Carangidae	1.7 (0.9)	0	12.0 (10.5)	0	0	0	0	0	0.3 (0.3)	0
Total pelagic fishes	2.3 (1.2)	0	12.0 (10.5)	0	0	0	7.7 (6.7)	0	0.3 (0.3)	0
Total fishes	8.7 (4.7)	5.0 (0.6)	12.0 (10.5)	0	1.3 (0.9)	3.0 (3.0)	8.0 (7.0)	32.0 (24.8)	1.0 (1.0)	25.7 (11.6)

Table 5. Density [mean nos. 31 m^{-3} (SE)] of presettlement and small pelagic fishes at three sites in lagoon of Bowden Reef when no slicks were present. Each site was sampled on three occasions in December 1987

Family	6 December			7 December			10 December		
	1	2	3	1	2	3	1	2	3
Reef fishes									
Atherinidae	6.3 (6.3)	0 (0)	0 (0)	0 (0)	0 (0)	1.0 (0.6)	1.0 (0)	11.7 (11.7)	1.7 (0.7)
Muraenidae	0 (0)	0.3 (0.3)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	11.3 (11.3)	1.0 (0.6)
Blenniidae	0.3 (0.3)	0.3 (0.3)	0 (0)	0 (0)	0 (0)	0.7 (0.7)	0.3 (0.3)	0.3 (0.3)	0.7 (0.3)
Pomacentridae	0.3 (0.3)	0 (0)	0.3 (0.3)	0.3 (0.3)	0.3 (0.3)	4.7 (0.9)	0 (0)	0 (0)	0 (0)
Total reef fishes	7.0 (7.0)	0.7 (0.7)	0.3 (0.3)	0.7 (0.7)	0.3 (0.3)	6.3 (1.7)	0.3 (0.3)	11.7 (11.7)	1.7 (0.7)
Pelagic fishes									
Carangidae	0 (0)	0.7 (0.7)	0 (0)	0.3 (0.3)	0 (0)	0 (0)	0.3 (0.3)	0 (0)	0 (0)
Total pelagic fishes	0 (0)	0.7 (0.7)	0 (0)	0.3 (0.3)	0 (0)	0 (0)	0.3 (0.3)	0 (0)	0 (0)
Total fishes	7.0 (7.0)	1.3 (0.7)	0.3 (0.3)	1.0 (1.0)	0.3 (0.3)	6.3 (1.7)	1.0 (0)	11.7 (11.7)	1.7 (0.7)

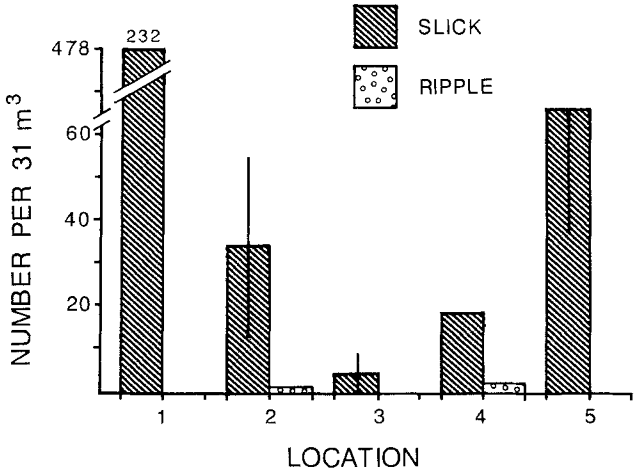

Fig. 9. *Aurelia aurita*. Density (mean ± SE, $n = 3$ seines) in slicks of Langmuir circulations and adjacent ripples water in lagoon of Bowden Reef. SE for slick at Location 1 was 232

which carangids were absent. Hence, concentration of some species in slicks may relate to an association with gelatinous zooplankton.

Hypoatherina sp. (Atherinidae) was the most abundant fish captured at three fixed sites in the lagoon, when no slicks were present (Table 5). Variation in abundance was high within sites. In most cases the standard error for atherinids was 60 to 100% of the mean. Aggregations of 30 to 50 fish (15 to 24 mm SL) were typically captured in a single seine, while other replicate seines often had no fish. This corroborated with the sampling in and out of windrows, in that atherinids swam in aggregations that did not relate to small-scale oceanographic features. With the exception of a few individual carangids and a small muraenid, the other fish caught at fixed sites were 2 to 3 mm long (blenniids and pomacentrids).

Discussion

Tidal fronts

Bowden Reef lies in the path of a north to south mainstream flow (Williams et al. 1984). Within 2 km of Bowden Reef the slicks of tidal fronts were generated by the reef. Slicks influenced the distribution patterns of fishes and zooplankton. Fronts and associated slicks were not stationary, but moved in response to changes of the tide. The reef, therefore, is a larger target for presettlement of fishes than its topography would suggest, due to a "halo" of localised oceanographic features. Fishes may aggregate passively in the convergences of fronts, or respond to the presence of a front for purposes such as feeding; factors influencing aggregation are discussed in Kingsford (1990). Above average concentrations of food could be the reason why highly mobile presettlement fish remain in association with slicks. This has been argued for the slicks of internal waves also (Kingsford and Choat 1986).

The most dramatic example of the movement of slicks was a front which formed off the north-west corner of the reef. In some conditions this was observed to orientate in a north-west direction on ebb tides and south-west on the flood. While rotating it extended over 1 km from the reef. As a consequence, presettlement fish associating with this slick may be transported toward the reef. The intensity of convergence in the front (that results in a slick) needs to be investigated further during periods of tidal change (e.g. ebb to flood); the convergence may be weakest at this time.

Because of the dynamics of tidal fronts, presettlement fishes may respond more strongly to the presence of a reef through comparatively distant oceanographic cues than they do from direct observation of the reef using visual senses. It is not known how smell or hearing influences movements of presettlement fishes. Models which simulate "larval drift", and the probability a fish has of meeting a reef, should consider the reef as a larger target because of a "halo" of localised oceanographic features to which the fish may respond. This may influence the chance a fish has of settling successfully. Furthermore, the southward movement of presettlement fishes following the prevailing flow is likely to be staggered, since fishes may respond to hydrological features near reefs. Some presettlement fishes may remain in waters close to their natal reefs because of small-scale hydrological features around the reef and the behaviour of the fishes. For example, Kingsford and Choat (1989) found that some types of fish remain close to reefs regardless of the distance a reef is situated from the mainland, across a continental shelf.

A major implication of our findings is that presettlement fishes which are swimming in the prevailing flow among reefs may become aggregated into patches within at least 2 km from a reef. The halo of influence by tidal fronts may also depend on the size of a reef. Assuming that the late-stage presettlement fishes leave slicks that are close to the reef, the organisation of fishes in fronts may decide whether settlement is a large rapid event or, in the absence of fronts, a more gradual input of potential settlers. Moreover, small-scale hydrological features probably influence local settlement patterns on reefs.

Studies of recruitment patterns that encompass a number of reefs have led some investigators to conclude that large patches of presettlement fishes drift down the continental shelf of the GBR (up to 100 km: Doherty 1987). There are, however, other explanations for such patterns of recruitment. For example, regional similarities in the timing of spawning could equally explain concurrent settlement events. This is particularly true for fishes that spawn according to phases of the moon (e.g. Doherty 1983) and which are of very similar length at presettlement phase. Separate concentrations of presettlement fishes around individual reefs may settle at the same time, giving the impression of an extensive uniform patch among reefs. More information is required on the distribution patterns of the presettlement fishes themselves.

The arrival of a slick on a reef may influence the diet and feeding of diurnal planktivores (see Kingsford and MacDiarmid 1988). Depending on the size of presettlement fishes, the consequences of movement toward a reef may be quite different. For example, preflexion and flexion fishes may be eaten, while juveniles and well-formed postflexion fishes may settle.

Williams et al. (1988) suggest the interaction between ichthyoplankters of reef and non-reef species should be considered. Such interactions are expected to be marked in slicks where concentrations of fishes are high and nearest-neighbour distances are relatively small; for example, predators may include small belonids, carangids, and sphyraenids. Indeed a cursory examination of the guts of five presettlement monacanthids in slicks revealed that some had consumed preflexion and postflexion fishes. Therefore, important interactions may occur among different ontogenetic forms (e.g. preflexion and juvenile forms) within ecological categories, and among categories such as presettlement reef fishes and small pelagic fishes. Interactions among ichthyoplankters and other zooplankton may be profitably studied in hydrological features such as slicks (see Turner et al. 1985, Kingsford 1990).

A variety of reef fishes were captured in this study. However, compared to the total number of fish groups recorded on reefs of the central GBR they only represent a small portion; reasons for this include the following. (1) The reproductive products of many species may not have been present in the plankton during the time of the study or in the area of Bowden Reef; (2) presettlement fishes of many families are not found at the surface or only move toward the surface at night (Leis 1986, Kingsford 1988); (3) attributes of the sampling equipment.

High concentrations of presettlement fishes were found in surface waters of the GBR. It is sometimes commented that concentrations of small pelagic and presettlement fishes are low in tropical waters (Leis in press). Converting our maximum concentrations to the units used by Leis (1 000 m^3) we recorded some very high values (483 to 2 774/1 000 m^3; total fishes). Highest average densities of mullids, pomacentrids and monacanthids were 290/1 000 m^3 in slicks and $<32/1\,000$ m^3 in rippled areas. Hence, although average densities of presettlement fish may be low when averaged over very large volumes of water, very high concentrations can be found in the slicks marking tidal fronts. This suggests that investigators should stratify their sampling according to hydrology (where possible), if accurate pictures of presettlement fish distributions are to be resolved.

Current patterns were studied near to and offshore from Bowden Reef. Regarding general flow, it was concluded that in practice there were no such thing as undisturbed uniform far-field water currents in a reef-matrix system. Bowden Reef is surrounded by reefs, and these influence the "far-field" currents, i.e., the currents in inter-reefal waters. Shelf-scale tidal models (e.g. Church et al. 1985) predict phase differences of a few minutes between tidal currents at sites a few kilometres apart in the Great Barrier Reef matrix. These models appear to be unrealistic, since our observations and those of Wolanski et al. (1989) revealed differences of up to 2 h between tidal currents at sites a few kilometres apart. The influence of mazes of reefs must be incorporated into oceanographic models of flow.

Langmuir cells in lagoon

Within the lagoon of Bowden Reef, fishes overall showed no consistent relationship with the presence of the slicks of windrows. This was explained according to the taxonomic group of fish and ontogenetic form. For example, *Hypoatherina* sp. of 15 to 24 mm SL were found in large aggregations throughout the lagoon, with distributions apparently unrelated to the slicks and the ripples of windrows. Moreover, they were caught in large aggregations in the absence of slicks. Preflexion pomacentrids showed a similar pattern, that may have related to mass hatching from demersal nests on coral outcrops throughout the lagoon. More research is required on the influence of Langmuir circulations on fishes and other zooplankters, since heterogeneous data prevented us from making formal analyses. Higher numbers of *Hypoatherina* sp. were always found in the lagoon compared to outside waters within 2 km of the reef. This concurs with the work of Schmitt (1986), who reported that atherinids spend most of their early life history very close to the reef. Similar to the observations of Hamner and Schneider (1986) in the Bering Sea, medusae were found in very large aggregations in the slicks of windrows. Juveniles and postflexion carangids were most abundant in slicks, and these slicks generally contained high concentrations of medusae. Very high densities of *Aurelia aurita* in slicks could have severe implications for small presettlement fish, since these jellyfish are voracious feeders on ichthyoplankton (Möller 1980, Van der Veer and Oorthuysen 1985).

The slicks of windrows are not as well defined as those of tidal fronts. Furthermore, the streaky slicks of windrows (see Faller and Auer 1988) makes it difficult to determine if one is in or outside slick or rippled areas. Dye experiments have demonstrated that windrows coalesce into one another and are not independent. Our inability, at times, to make a clear distinction between slick and ripple may have confounded some comparisons. Windrows were not examined outside the lagoon for logistic reasons, so it is not known how they influenced the distribution of fishes. Because the transport in windrows is parallel to the direction of the wind, they clearly have the potential to be important in influencing the movements of fishes in surface waters over the shelf (Shanks 1986, Kingsford 1988, 1990). Contrary to tidal fronts, however, windrows have no relationship to reef topography.

Conclusions

Important small-scale oceanographic features were found in the vicinity of coral reefs (<2 km). Tidal fronts influenced the distribution and movements of presettlement fishes and zooplankton. It was suggested that juvenile and postflexion presettlement fishes are attracted to slicks because of the high densities of planktonic food in them. Weak-swimming fishes may simply be caught in the convergence of slicks. Slicks were observed to move toward and away from the reef. A consequence of aggregation in some fronts may be transport toward the reef. When fronts swing away from the reef, off-reef transport is also possible. Because presettlement fishes aggregate in the slicks of tidal fronts generated by reefs, they respond to the presence of reefs through comparatively distant oceanographic features. Therefore, our perception of the size of a reef as a settlement site should be altered to include reef-induced fronts. Fronts have the potential to behave like giant arms, aggregating fishes and plankton from offshore and transporting them toward the reef. This has important implications for models of "larval drift". Indeed, patches of presettlement fishes may be organised near reefs on many occasions rather than arriving in near-reef waters as a large unit due to hydrographic processes or the behaviour of fishes. We conclude that using recruitment surveys as a means of inferring the structure of presettlement fish patches in the pelagic environment should be treated with caution.

There was no consistent relationship between abundance of presettlement fishes and the slicks of windrows in Bowden lagoon. Different groups of fish appear to respond to these oceanographic features in different ways. However, our data on fishes in Langmuir circulations should be treated with caution due to heterogeneous variances.

This study emphasises the importance of stratifying sampling according to hydrographic features both inside and outside lagoons, where possible. Linear features probably influence the distribution and movements of presettlement fishes among reefs as well as close to them. Windrows (Barstow 1983), internal waves (Kingsford and Choat 1986, Wolanski 1986), near-reef topographically-induced fronts (Wolanski and Hamner 1988 and present study), and oceanic fronts (Le Fèvre 1986) may all play important roles. Advection according to prevailing flow, undisturbed by reefs, should not be considered the only important (or even dominant) hydrological influence on the distribution, movements, and survivorship of presettlement fishes.

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