รูปแบบรายงานวิจัยฉบับสมบูรณ์ แบบที่ 1

รายงานวิจัยฉบับสมบูรณ์

Environmental factors controlling the success of coral reefs in coastal Thailand: salinity as a structuring agent for reef assemblages

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Project Title:

Environmental factors controlling the success of coral reefs in coastal Thailand: salinity as a structuring agent for reef assemblages

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Abstract

Corals in near-shore environments are particularly vulnerable to the effects of climate change, especially in those locations where the coastal fluvial landscape has been altered by human activities. The investigation of salinity responses of corals from reefs exposed to river plumes provides insight into the structuring role of monsoonal flooding on coral assemblages and their long-term prognosis. In this study, the effects of hyposalinity exposure on corals acclimated to nearshore conditions were examined for five genera of hard corals. Fertilisation success, larval survivorship and settlement success showed clear trends amongst genera. Unsurprisingly, those species of massive corals that are most common in shallow reef flat environments were the most tolerant of salinity stress as larvae. The most susceptible species were the branching and table Acropora. These trends were repeated in adult corals subjected to prolonged hyposaline conditions. Measurement using tissue lipid concentrations as a proxy for energy reserves reflected the same patterns of stress tolerance. Duration of exposure at moderately low salinities (22-25PSU) was a critical transition factor for survivorship of the most sensitive species: pulses of low-moderate salinity such as might be associated with severe rainfall events were well-tolerated, but prolonged exposure caused rapid declines in lipid reserves and survivorship. These results demonstrate that severe flooding events, such as affected the Gulf of Thailand in 2011 can drastically change the community structure of nearshore reefs and have lasting impacts on the function and replenishment of crucial nearshore habitats.

Keywords: Coral, salinity, lipid, stress, environmental factors

Introduction

Reef-building corals are osmoconformers – that is, they do not possess a constant cellular osmolarity, but respond to dynamic changes in their environment, and gain cellular water in hypotonic conditions. All cells require a somewhat stable environment to function optimally; large shifts away from optimum osmolarity can cause changes in macromolecular structure and metabolic function. Therefore, salinity flux can cause extremely large changes in the cellular chemistry of corals and negatively impact on their relationship with the symbiotic zooxanthellae that make it possible for them to construct reef platforms (Mayfield & Gates, 2007).

Corals in near-shore environments are particularly vulnerable to the effects of climate change, especially in those locations where the coastal landscape has been altered by human activities. Corals in stressful environments are hampered by the high energetic cost of survival, whether due to coping with salinity stress, sediment removal or competition (Kleypas et al., 1999). Moreover, where no existing carbonate platform exists, dissolved calcium carbonate may be present at below saturation levels, thus increasing the cost of precipitation for the calcifiers.

When scleractinian corals lose the ability to calcify easily, they are unable to heal damage or to grow, rendering them vulnerable to invasion by pathogens; corals stressed to the point of growth failure certainly do not possess the large energy reserves required for reproduction. Energy reserves in corals can be estimated using a variety of proxies, providing insight into the capacity of the corals to combat stressful condition. More flux-tolerant species and those that are likely to succumb to prolonged hypo-salinity events can thus be identified by relative changes to the levels and composition of storage lipids before and after exposure to stress.

The replenishment process of coral reefs largely depends on the supply of planktonic larvae. Very little is known about large scale trends in coral reproduction and reproductive success in the Gulf of Thailand. It is known, however, that strong gradients in salinity can seriously compromise reproductive success and recruitment of corals to affected habitats. Lack of reproductive success and continued replenishment failures can render coral communities vulnerable to extinction even when those communities are composed of robust, flux-tolerant species (True, in revision). The larvae of broadcast spawning corals do not possess symbiotic zooxanthellae and do not feed whilst in the plankton; larvae must therefore rely on the lipid reserves bequeathed on them by their parent to settle and create their first skeleton. Depletion of these lipid reserves coping with hyposaline conditions may severely compromise the survivorship and settlement success of coral larvae.

Significance of the project

Coastal reefs in South East Asia are under increasing pressure as coastal development reduces shoreline protection and allows greater impacts from terrestrial runoff during wet monsoon seasons. As development pressure increases, more coastal forest is cleared and natural barriers to runoff are diminished. In addition to the nutrifying influence of coastal

agriculture, the effects of the terrestrial runoff on coral communities are measured mainly in terms of increased salinity fluxes and input of fine-grained terrigenous sediment (Wilkinson, 1999). Moreover, IPCC models of global climate change in the next century predict that monsoon rainfall in South East Asia will become more intense, exacerbating the vulnerability of coastal coral communities to flood events.

Most research on the effects of hyposalinity thus far has focussed on the impact of freshwater influx as a short-term stressor, tending to concentrate therefore on the lethality of different degrees of hyposalinity on indicator species. Even research examining the sub-lethal effects of low salinity has mostly failed to take account of evidence that coastal coral communities are exposed to seasonal episodes of low salinity and high turbidity resulting from monsoon floods. These episodes can be quite prolonged, often lasting for several months. The composition of coral communities is thus a reflection of both the resilience of their constituent species in the face of recurrent prolonged sub-lethal stress, and the vulnerability of species which cannot survive such conditions (but may occur in more benign environments close by). Knowledge of the tolerance limits of different coral species will therefore allow not only the real-time monitoring of the impact of changing conditions, but insight into the taphonomic processes affecting the coral communities.

Although potentially immortal, since they are able to replace damaged modules indefinitely, corals are vulnerable to habitat degradation and environmental impacts that cause stress or damage beyond their ability to repair. Replenishment of coral colonies lost to environmental impacts and natural processes is thus a vital process within coral ecosystems. Because corals in most parts of the world (including the Gulf of Thailand) tend to reproduce just before the start of the monsoon wet season, their replenishment may be compromised by climatic changes that may increase their exposure to salinity flux. Although there is little extant data on either larval survivorship or settlement success in hyposaline conditions, it is highly likely that the larvae are affected to an even greater degree than adult corals. Thus, it is important to examine the effects of hyposaline conditions on larval survivorship and settlement success to determine whether climate change will compromise the replenishment processes of coral ecosystems in the Gulf of Thailand.

Objectives

1) To investigate the effects of a major near shore environmental controlling factor (salinity) on the composition of coral communities and potential threats to ecosystem function and replenishment due to climate change;

2) To identify those species of corals that can be used as markers for monitoring changes in environmental conditions;

3) To identify which stages in the early life history of corals are particularly vulnerable to salinity stress and to examine the effects of hyposalinity on larval and juvenile survivorship and development.

Experiment 1:

1.1 Methods

In this study, we investigated the fertilisation success, larval development and settlement success of 5 species of hard corals from local reef communities exposed to 3 experimental levels of hyposalinity. Control salinity was ambient Gulf of Thailand inshore levels (32PSU); experimental levels were set at 28 and 24PSU (reported by Moberg et al (1997) to occur for significant periods in the Inner Gulf of Thailand). During a pilot study, it was determined that little additional information was gained from partitioning the study into finer intermediate salinity classes or to pursue extremely low salinities, since 100% mortality of larvae of all species occurred at salinities within 48 hours. In fact, the larvae of no species were able to tolerate prolonged exposure to hyposalinity conditions such as those measured on the reef flat at the time of the experiments (16-19PSU).

Coral gametes were captured as they were released from wild colonies of four common species (*Platygrya sinensis, P. daedalia, Favites abdita and Acropora hyacinthus*) during the annual spawning event at an inshore reef at Ko Mannai, Rayong Province. Gamete bundles were captured from 4-5 colonies of each species.

Figure 1 Egg/sperm bundles just prior to release during spawning

Sperm and eggs were then transferred to 2-litre culture vessels filled with seawater diluted to predetermined experimental salinity levels with sterile fresh water (bottled potable water); 3 replicate vessels were prepared for each species at each salinity. Since high sperm concentrations can be toxic, the volume of water containing the gametes was diluted until sperm concentrations were estimated to be optimal.

Figure 2 Egg/sperm bundles being collected by a research intern

Sperm and eggs were then transferred to replicate 2-litre culture vessels filled with seawater diluted to test salinity with sterile fresh water (commercial potable water).

Each culture vessel contained approximately 2000 eggs at the commencement of the experiment. Samples of approximately 40 eggs and/or larvae were pippetted out of the

culture vessels at 1-hour intervals for the first 4 hours (when critical developmental changes occur), and then every 12 hours for the first 2 days and every subsequent morning for the remainder of the experiment.

Culture vessels were supplied with light aeration and maintained in a shaded environment protected from direct sunlight. Water in the culture vessels was changed for freshly mixed test solutions every 6 hours for the first day, and every 12 hours thereafter. When larvae began to exhibit behavioral changes associated with settlement, pre-conditioned artificial settlement substrates were placed inside the culture vessels.

Concentrated sperm and egg mix
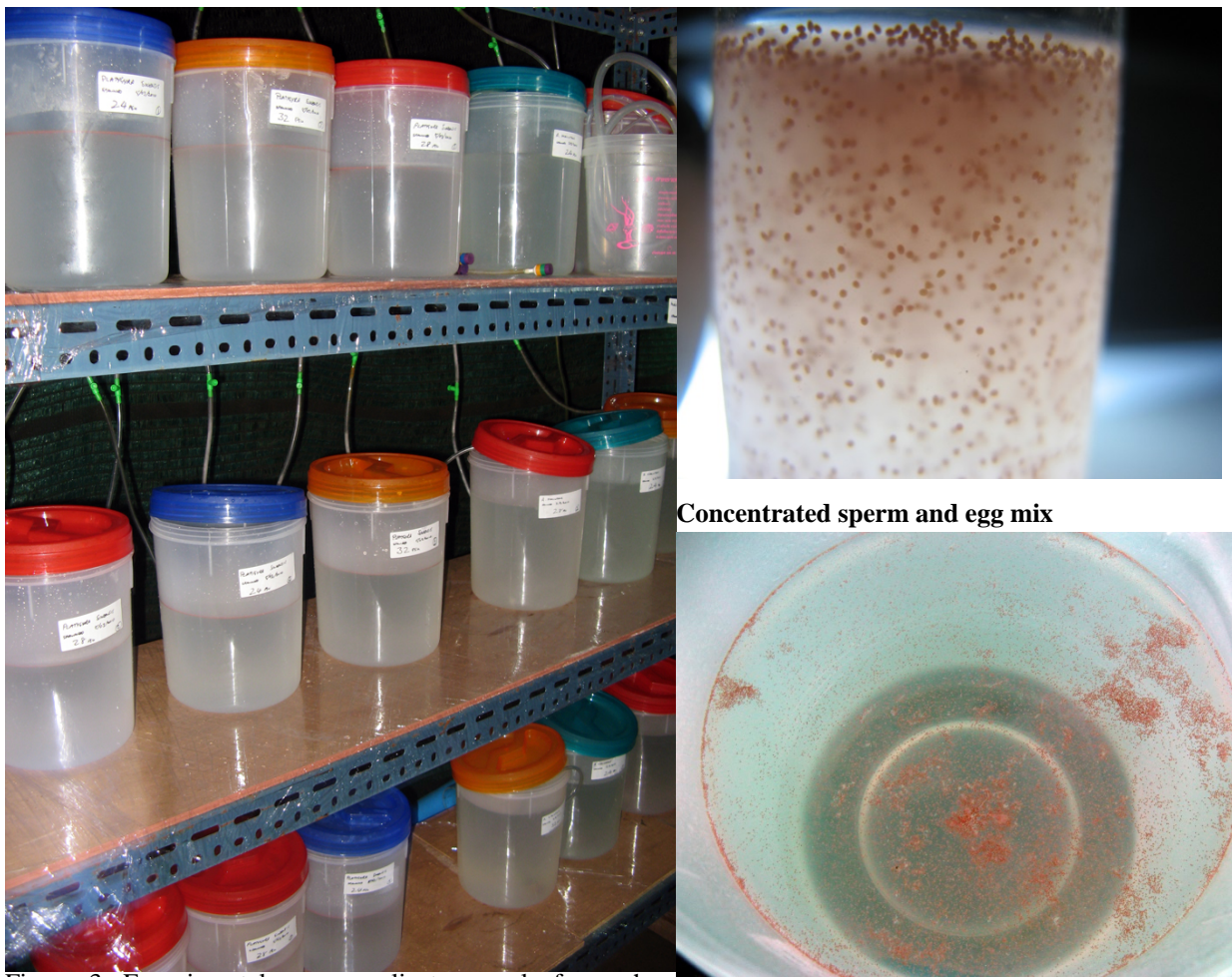
Figure 3. Experimental array; replicate vessels for each species and salinity were randomly allocated to slots in the array to prevent unintended bias

Fertilised larvae in the experimental array (note clarity of water, since excess sperm have been washed away

Rates of deformity and estimated populations in the culture vessels were recorded for each sample. Subsequent to settlement, photographs of settled larvae were made using a Nikon D70 digital camera mounted on a Wild™ stereo microscope. Estimates of numbers of settled larvae made at the same time. Numbers of settled larvae for each species were based on counts from 9 replicates each of circular settlement blocks ~5cm^2; counts included only larvae settled on the upper surfaces.
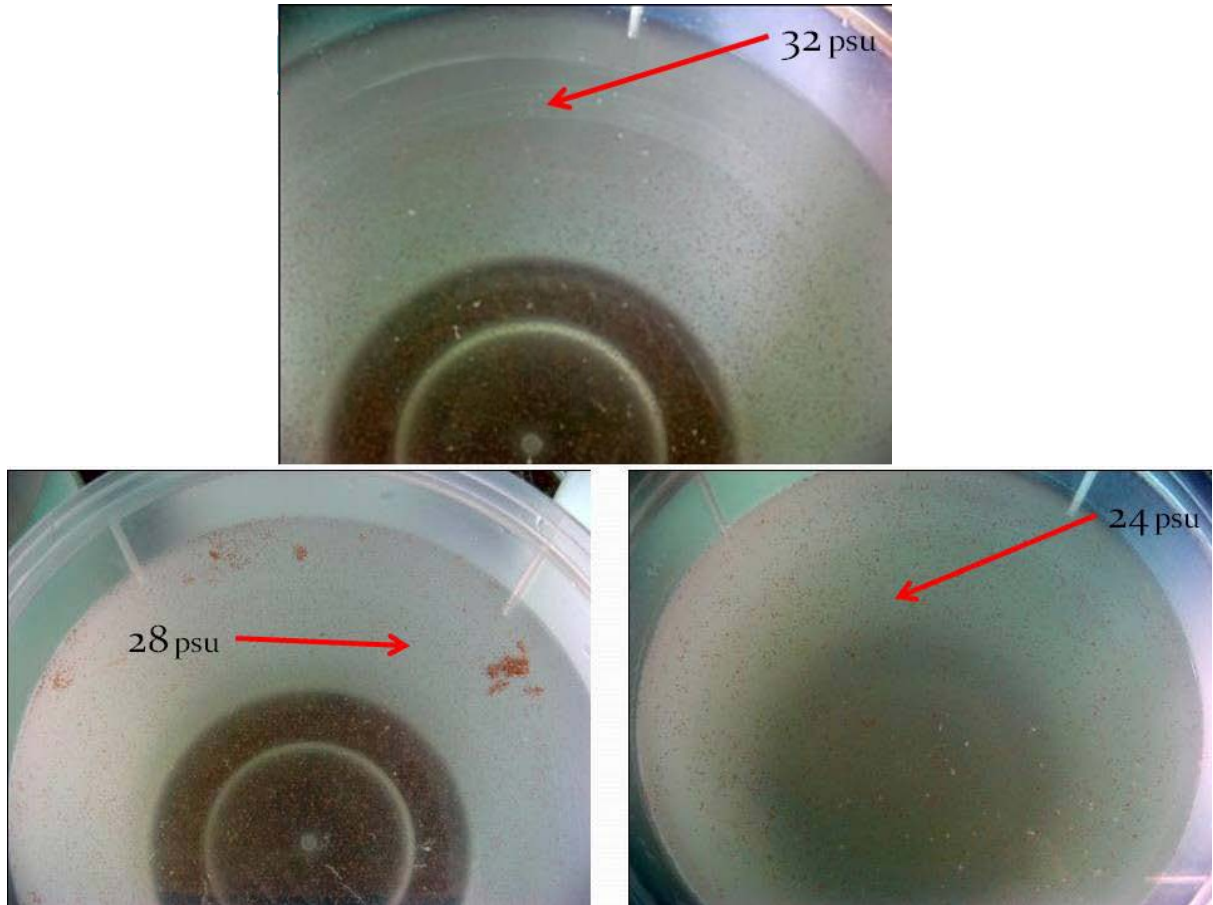
Figure 4 Larvae at lower salinities tended to clump together. Water qulity in th low salinity treatments was noticeably worse than the controls.

Platygyra – 32psu, 72 hours   *Platygyra* – 24psu, 72 hours
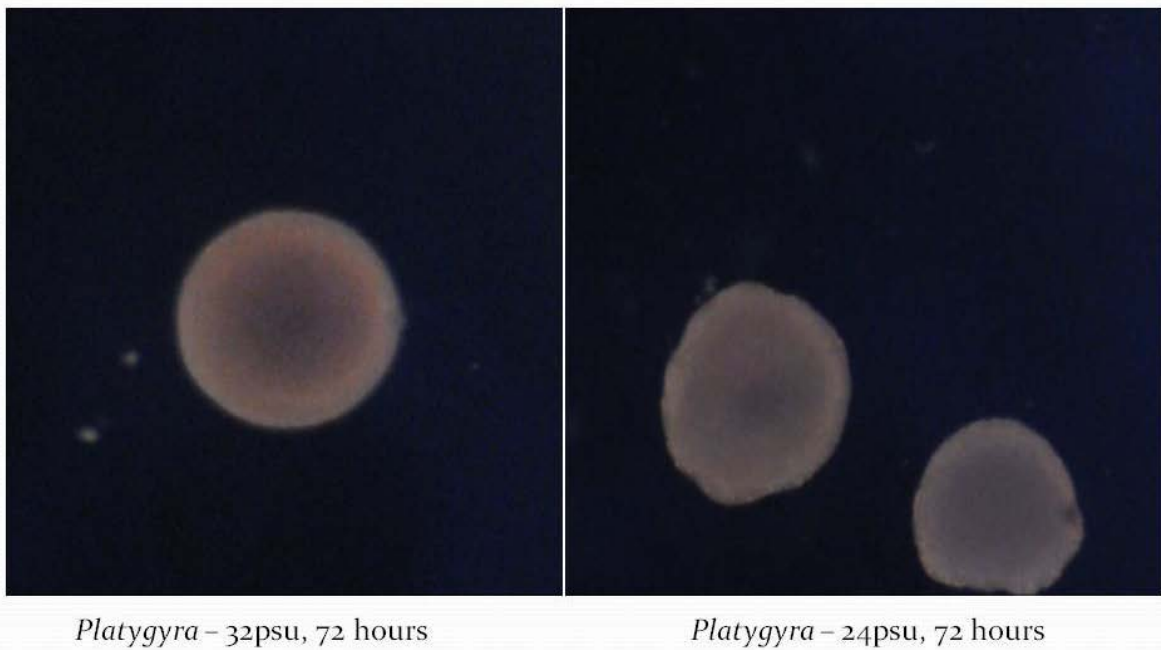
Figure 5   Larvae at lower salinities exhibited numberous developmental problems, including retardation and deformity

1.2 Results and Discussion

The rate of development of larvae of the different species was differentially affected by hyposalinity. Larvae of all species under control salinities reached settlement competency in 4-5 days, displaying characteristic behaviors and morphology. After the first day's development, few damaged or deformed larvae were observed amongst any species.


In contrast, even moderately reduced salinity caused significant retardation in the rate of larval development across species; moreover, increasingly high levels of deformity and damage were observed with decreasing salinity. Larvae of *Acropora* were most affected by hyposaline conditions and did not achieve full development under low salinity conditions.

Developmental deformity of larvae seemed to be associated with survivorship; initial high levels of larval deformity in the most stressful treatments corresponded with higher mortality. However, there appeared to be no clear relationship between species and rate of deformity (Figure 2).

Figure 6 Survivorship of coral larvae developing in different salinities; the vertical axis represents the proportion of the initial population (~2000 fertilised eggs) surviving at the end of each day. Arrows indicate settlement events.

Mortality amongst larvae in the hyposaline conditions was inversely proportional to salinity and varied amongst species (Figure 1); even a relatively slight reduction in salinity from oceanic standard (35 PSU) as shown by the 32 PSU treatment corresponded to a large reduction in larval survivorship. *Acropora* larvae perished at a much higher rate than did the faviid larvae, to the extent that the populations in the lowest salinity treatments died after only 3 days; while the larvae in the moderate treatment (28PSU) persisted for 4 days, they did not develop to full settlement competency (survivorship to late planula stage dropped to <5% at 28 PSU and zero at lower salinities).

It appears that settlement success of larvae exposed to lower than usual salinities varied between species; those that could be found as adults on the reef flats were able to settle and commence calcification of their exoskeleton even in salinities as low as 24PSU, albeit in much reduced numbers (Table 1). Settlement success of larvae exposed to lower than usual salinities varied between species; those that could be found as adults on the reef flats were able to settle and commence calcification of their exoskeleton even in salinities as low as 24PSU, albeit in reduced numbers and a day later than those at the control salinity.

Table 1: Settlement density of coral larvae reared at different salinities (per 10cm^2 settlement surface).

Species/Salinity	32PSU	28PSU	24PSU
Acropora hyacinthus	24 $\pm$7	0	0
Favites abdita	150 $\pm$25	70 $\pm$ 21	16 $\pm$ 6
Platygyra daedalea	134$\pm$ 19	41 $\pm$ 16	9 $\pm$ 7
Platygyra sinensis	118 $\pm$39	51 $\pm$ 15	18 $\pm$ 24

Settled larvae at low salinities were observed to be smaller and paler than the controls, especially amongst the *Platygyra*. Not all settlement blocks in the lowest salinity treatment were successfully settled. Where settlement did not occur in the lower salinity treatments, larvae were observed to have exuded copious amounts of mucus and perished (whether the mucus production occurred prior to death is unclear: dead cells appeared suddenly, clumped and surrounded by mucus).

Settlement of larvae of *F. abdita* and *P. sinensis* at lower salinities (28 and 24PSU) appeared to be slightly retarded compared with those in the control salinity; while a few settled larvae were observed on day 3, the majority settled on day 4 (Figure 1). Settled larvae at low salinities appeared to be smaller than the controls, although it was not possible to measure them with the equipment available.

The replenishment process of coral reefs largely depends on the supply of planktonic larvae. Very little is known about large scale trends in coral reproduction and reproductive success in the Gulf of Thailand. It is known, however, that strong gradients in salinity can seriously compromise reproductive success and recruitment of corals to affected habitats.

Figure7 Larval development of *Platygyra sinensis* (Faviidae) cultured under different salinities. Percentages represent the average of 3 replicate samples.
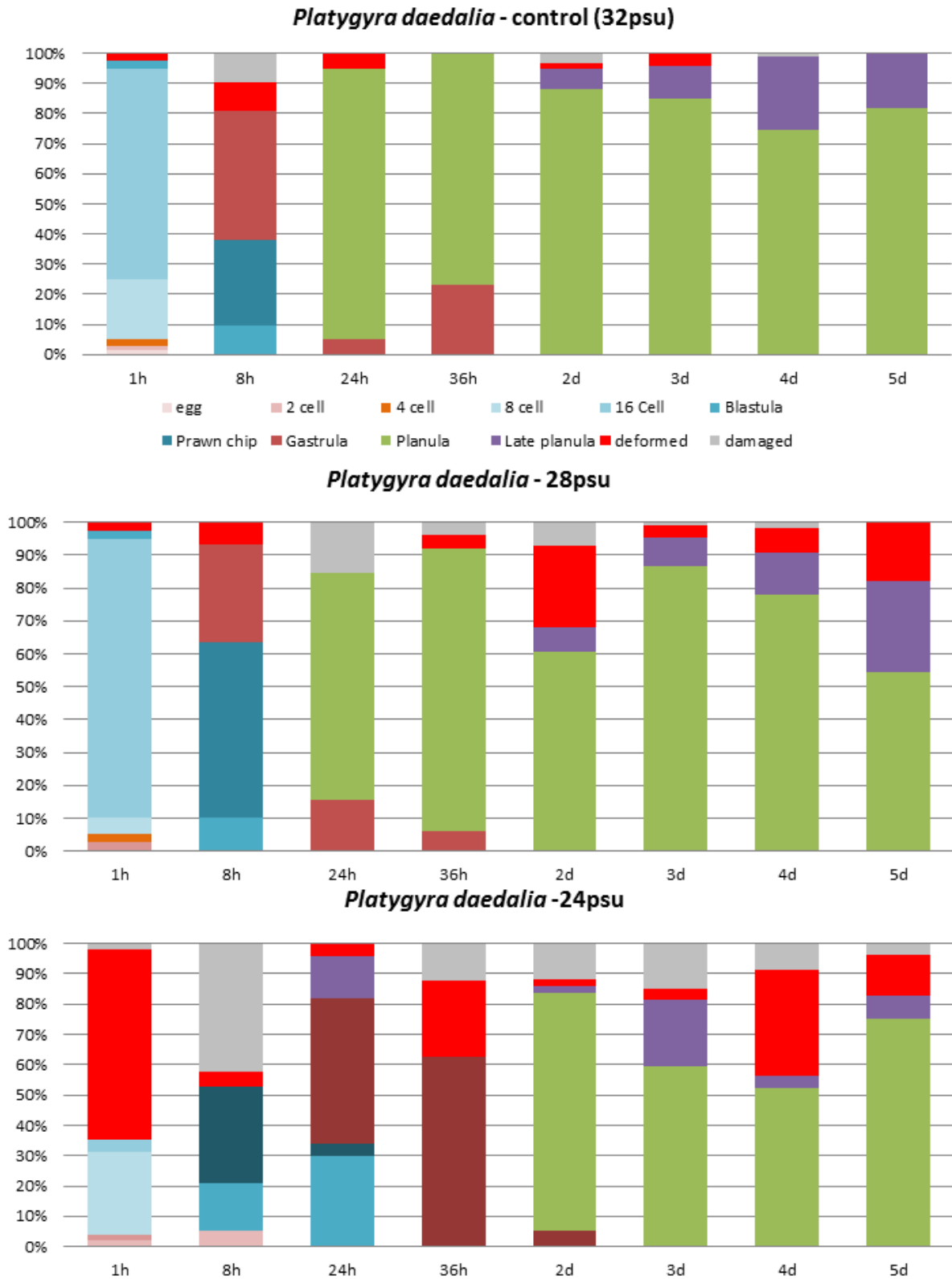
Figure 8 Larval development of *Platygyra daedalia* (Faviidae) cultured under different salinities
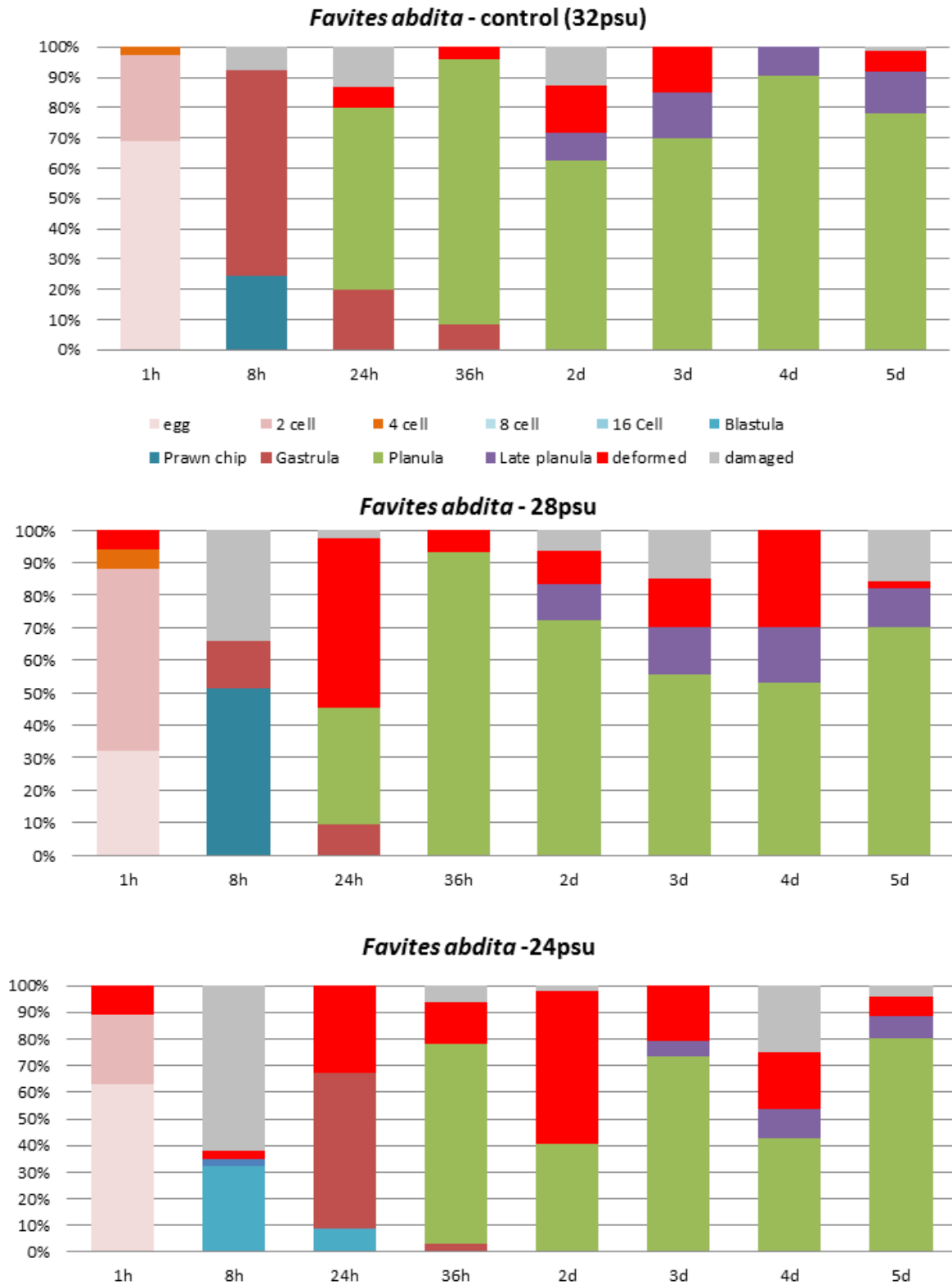
Figure 9 Larval development of *Favites abdita* (Faviidae) cultured under different salinities
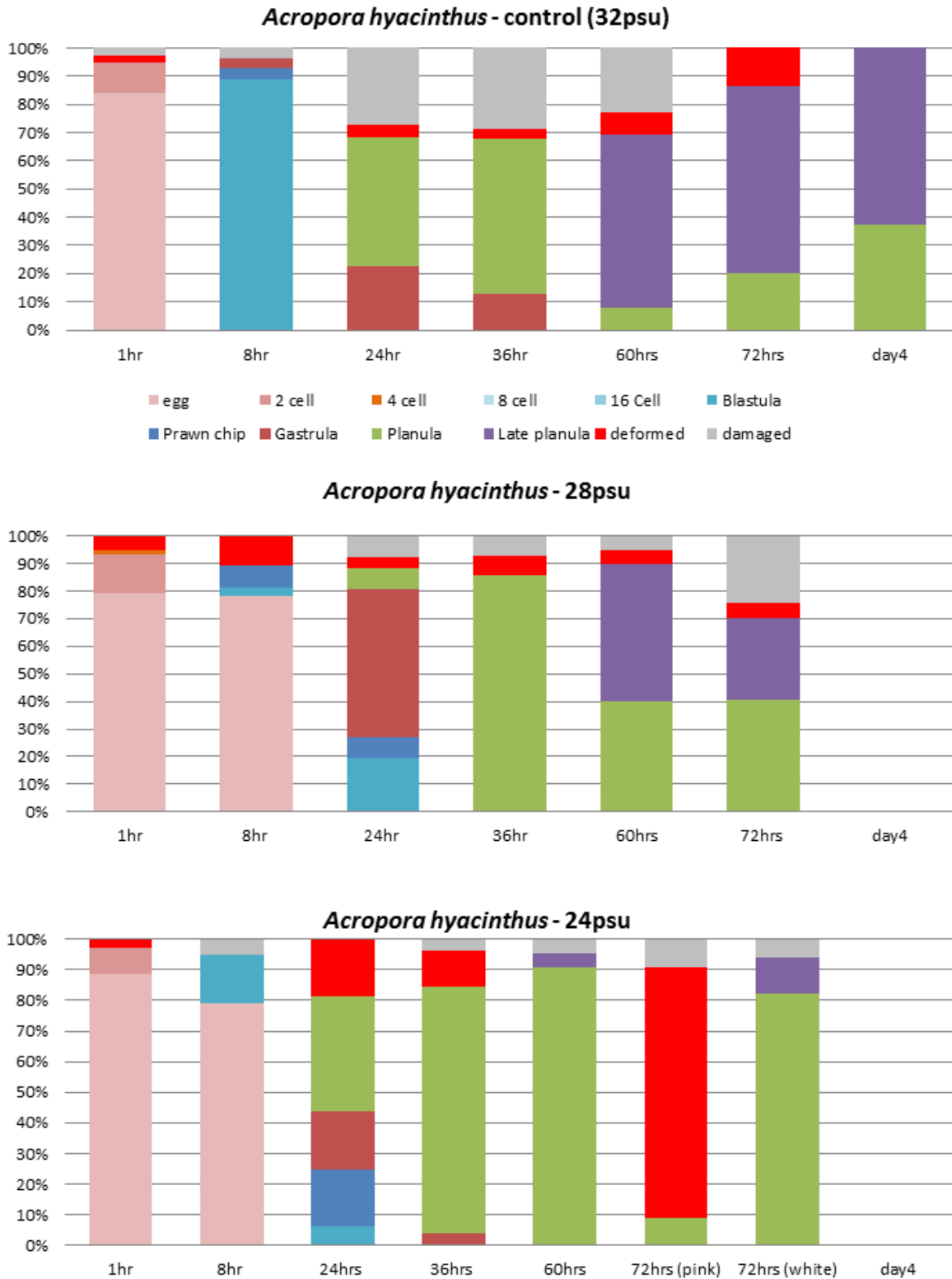
Figure 10 Larval development of *Acropora hyacinthus* (Acroporidae) cultured under different salinities
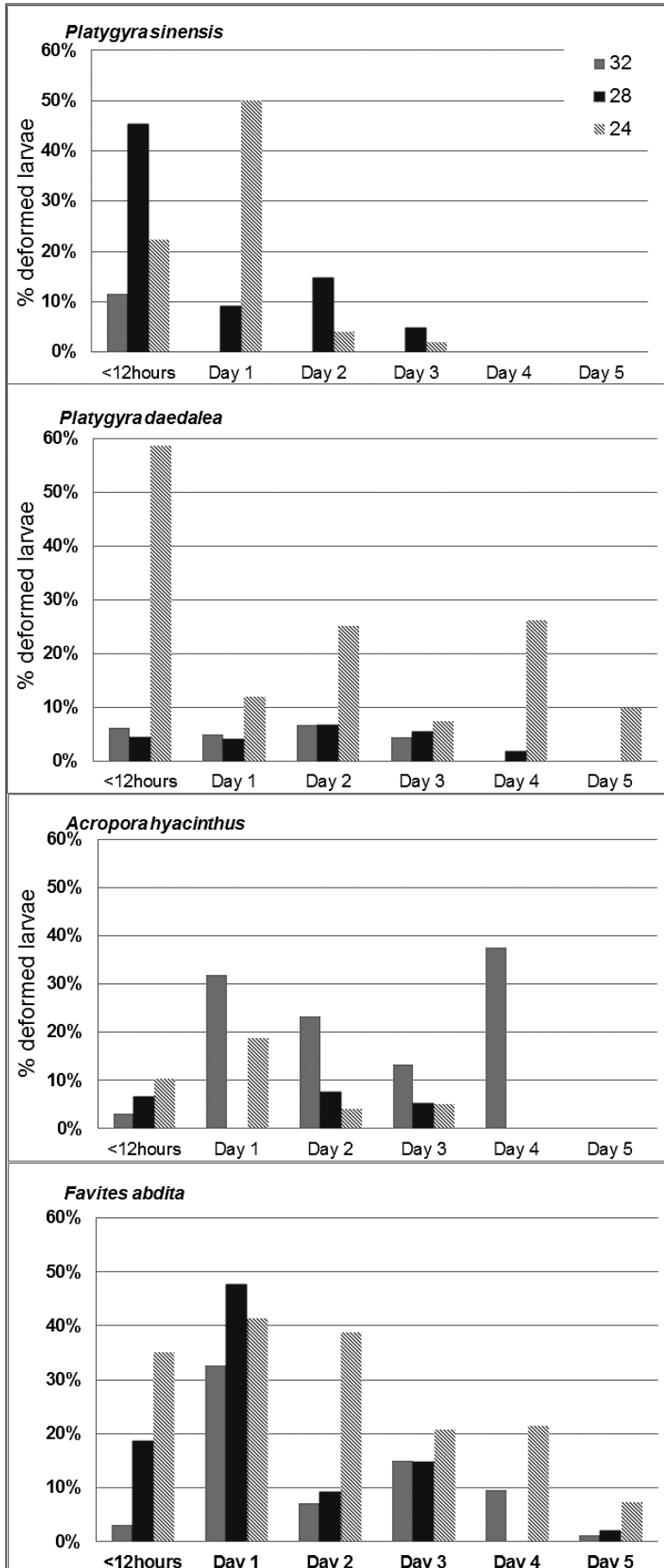
Lack of reproductive success and continued replenishment failures can render coral communities vulnerable to extinction even when those communities are composed of robust, flux-tolerant species (True, unpublished).

These results indicate that:

1) heavy rainfall events can exert a strong control on the reproductive success of hard corals, since larval development takes place at the surface of the water column;

2) successful recruitment pulses for many species may only occur in those years where the wet monsoon is delayed;

3) an increase in coastal runoff due to clearing of vegetation and climate change may remove certain vulnerable species from near-shore reef communities.

Figure 11 Degree to which hyposalinity appears to have affected development of coral larvae. Deformities appeared even amongst larvae reared in the reference salinity, suggesting that attrition among larvae under normal conditions is high. Some low apparent rates may be due to the rapid breakdown of unviable larvae of some species.

The larvae of broadcast spawning corals do not possess symbiotic zooxanthellae and do not feed whilst in the plankton; larvae must therefore rely on the lipid reserves to settle and create their first skeleton. It was not possible to evaluate changes in the lipid budgets of larval corals during this study, due to the paucity of larvae spawned after the 2010 mass bleaching event (which interrupted coral reproduction for more than two years).
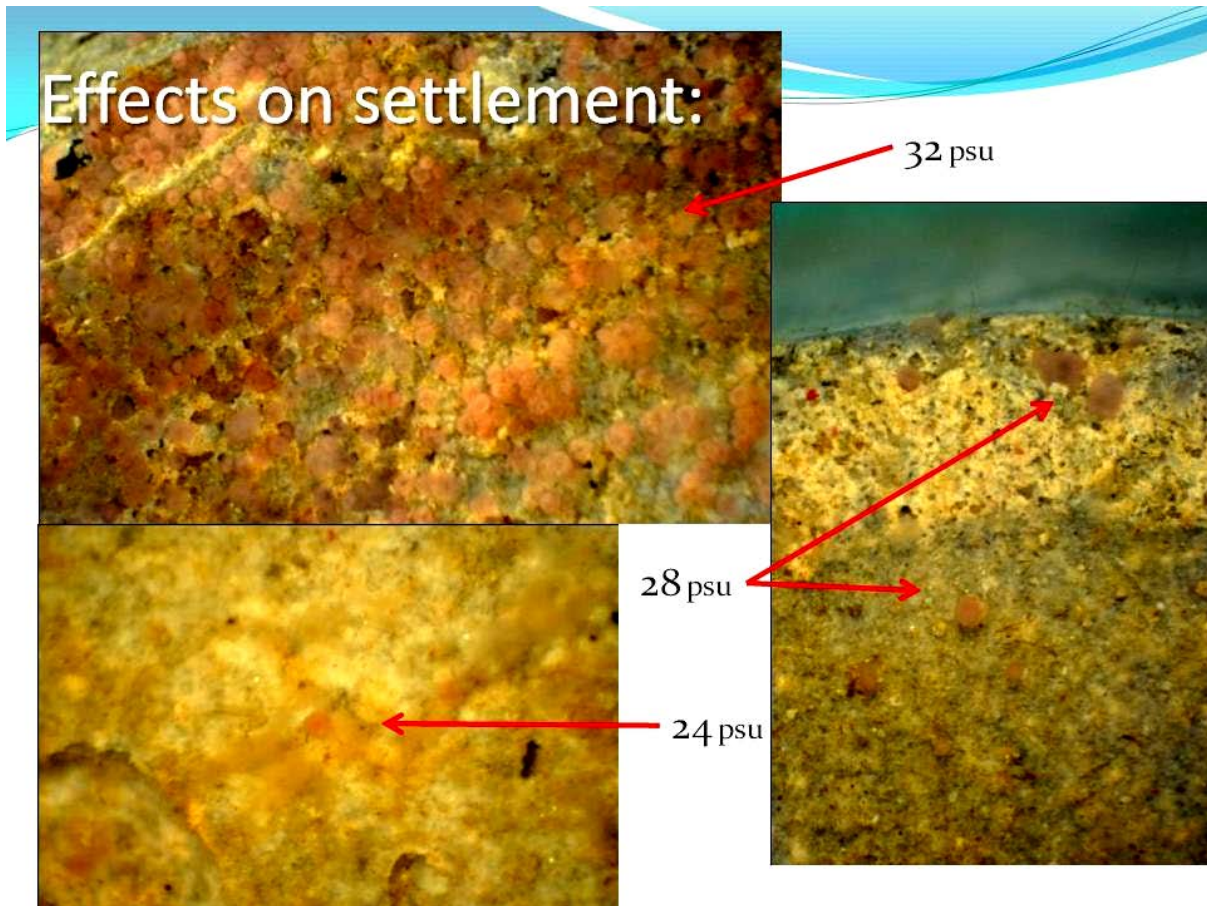
Figure 12 Differing settlement patterns of coral larvae reared under control (32psu), mild (28psu) and strongly (24psu) hyposaline development conditions

These results of this study, however, indicate that 1) heavy rainfall events can exert a strong control on the reproductive success of hard corals, since larval development takes place at the surface of the water column; 2) successful recruitment pulses for many species may only occur in those years where the wet monsoon is delayed; 3) an increase in coastal runoff due to clearing of vegetation and climate change may remove certain vulnerable species from near-shore reef communities.

Experiment 2:

2.1 Methods

Coral tissue is rich in lipid, in both structural (e.g. cellular membranes) and storage roles. Stimson (1987) reported that lipids of various classes constituted between 30-40% of the dry tissue weight in Hawaiian *Pocillopora* colonies from shallow water. This worker also reported that colonies kept in reduced light presented lower growth rates and lipid levels than unshaded colonies. In a survey of 15 cnidarians (mostly scleractinians), Yamashiro et al. (1999) found lipids to constitute between ~15% and ~30% of the dry tissue weight of their organisms. Their reported value for *Pocillopora* concurred with that of Stimson (1987), but in general, zooxanthellate scleractinian corals did not contains substantially greater amounts of lipids than other cnidarians.

To discover the sublethal effects of hyposalinity on adult corals, we exposed samples from 5 colonies of each of five scleractinian coral species (*Acropora muricata, Platygyra sinensis, Pocillopora damicornis, Favites abdita and Turbinaria frondens*) to different degrees of hyposalinity and measured changes in total lipid concentration of their tissues. Samples were obtained from 5m depth in a shallow fringing reef community in Chumphon Province, southern Thailand.

One of the most commonly discussed "symptoms" of stress in corals is bleaching. Bleaching in scleractinian corals is defined in terms of zooxanthella loss (Jones 1997). Since the photosynthetic pigments of zooxanthellae provide most of the colour observed in a coral colony, the loss of these symbionts is an unmistakable sign that some great stress has occurred. Previous experimentation had indicated that 24 hour exposure to salinities lower than 16PSU were invariably fatal to *Acropora*. In a pilot study, 3 of 5 *Acropora* and 4 of 5 *Pocillopora* nubbins survived 24 hour exposure to 18PSU and subsequent return to ambient salinity, as did 100% of nubbins from the other species.

Prolonged exposure to 18PSU salinity (3 days) resulted in 100% mortality for *Acropora* and *Pocillopora*, and signs of tissue withdrawal in *Turbinaria* and *Platygyra*. Experimental salinities were therefore fixed to levels that were undoubtedly stressful, but unlikely to be fatal for the subjects over a 24 hour period (i.e. 32 (control), 24 and 18PSU). The experiment was allowed to run for 24 hours, during which observations were made of behavioural (tissue withdrawal or absence of feeding) or gross physical changes (bleaching, tissue sloughing, copious mucus production), after which all samples were removed. Samples were collected from a coastal reef at a depth of 3m. Six subsamples from each colony were divided into small (~5-6cm^2) pieces and mounted on small concrete pedestals (previously soaked in fresh water for 2 days). Samples were kept in fresh flowing seawater for 1 week to heal before being used in experiments.

The experimental apparatus was composed of six identical closed recirculating systems. In each of the recirculating systems, six independent 2100 ml cylindrical plastic containers were connected to upper and lower reservoir tanks in each system. Water was circulated by a 12 volt aquarium pump in the lower reservoir tank, which also contained conditioned aquarium bioballs (for filtration and nitrification). Water was pumped from the lower reservoir tank to the upper reservoir tank at a rate of 20l.sec^{-1}. Gravity-fed water flowed from the upper reservoir and was directed to the bottom of the test chambers by inert silicon tubing. Coral nubbins were assigned to random chambers for each apparatus such that each set had exactly one nubbin from each colony. Water in each experimental unit was changed for fresh seawater once, and 2 hours later changed to target salinity; target salinity was achieved by adding potable water to the lower reservoir of each unit over a period of approximately ½ hour.

Samples were fixed in liquid nitrogen at the completion of the experiment. Surface area of samples was determined using the foil method (Marsh 1970); volume of tissue was estimated using either extrapolation (*Acropora*, which has a perforate skeleton – i.e. tissue all the way to the centre of the branch) or from the thickness of the tissue layer (all others). Tissue was removed from the coral skeletons using the Waterpik™ method (Johannes & Wiebe 1970). The resultant aliquot was centrifuged at 3000 rpm for 12 minutes. The supernatant containing the macerated coral tissue was pipette out to a 250ml flask. Total lipid content of the coral tissue was estimated using a gravimetric method (Folch et al, 1957). The total weight of lipid was standardized against estimated tissue volume.

2.2 Results and Discussion

Nubbins from adult corals exposed to 24 hours of hyposalinity exhibited various behavioural changes associated with stress: e.g. heavy mucus production, cessation of feeding activity. Nubbins at the control salinity exhibited "normal" behaviour for corals in aquariums: polyps and tentacles were extended for prolonged periods and mucus production was minimal. Corals kept at the 24PSU level retracted their polyps and exhibited no signs of activity, but neither did they exude mucus at higher than normal rates. Likewise, corals kept at the lowest (18PSU) salinity exhibited no signs of activity; some mucus was observed in the *Acropora* and *Pocillopora* groups, although output was not continuous.

It is noteworthy that *P.sinensis* and *A. muricata* exhibited apparent changes in tissue lipid concentration due short-duration exposure to lowered salinity (Figure 3), although only the data for *Acropora* were statistically significant. *Acropora* showed significant differences between 32 and 24PSU, and between 24 and 18PSU (1-way ANOVA). No statistically significant difference (1-way ANOVA) in lipid concentration of coral tissue was found between salinity treatments for *P. sinensis, P. damicornis, F. abdita* or *T. frondens* (although *Turbinara* exhibited a difference at $\alpha=0.1$). In the case of *Platygyra* and *Pocillopora*, this appears to result from the relatively high degree of between-colony variability in lipid concentration.
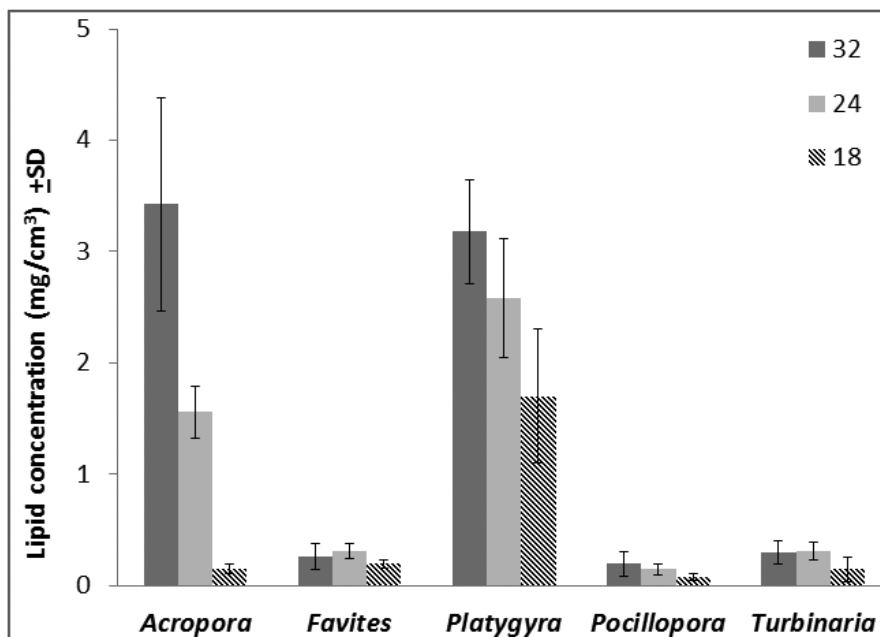
Figure 11 Differences in lipid concentration of coral tissue exposed to differing levels of hyposalinity (32PSU is the reference salinity).

Visual inspection of the data suggests that larger sample sizes may support the statistical validation of apparent biological trends for some of these species. Of the species studied here, only *Favites* and *Platygyra* occur regularly on the reef flat (albeit *Platygyra* prefers the deeper sections of the reef flat) and are thus exposed to strong salinity flux. *A. muricata* is only seldom found inshore in Thailand; its intolerance of even short term hyposalinity appears to offer a good explanation for this.

Duration of exposure at moderately low salinities (22-25PSU) thus appears to be a critical transition factor for survivorship of the most sensitive species: pulses of low-moderate salinity such as might be associated with severe rainfall events were well-tolerated by the sensitive *Acropora* sp., but prolonged exposure caused rapid declines in lipid reserves and also survivorship (True, unpublished data). Hyposaline conditions and the re-suspension of polluted sediments by typhoons may be thus determining factors in fertilisation and settlement success (cf. Heyward 1988; Tomascik 1991; Smith *et al.* 2003; Reichelt and Harrison 2005). Even if the gametes successfully fertilise, however, low salinities and poor water quality may render the energetically expensive creation of skeletons too costly for broadcast spawners.

The ubiquitousness of salinity-sensitive species such as *Acropora hyacinthus* in coral assemblages of the eastern Gulf of Thailand (from Chonburi, eastwards: Chansang et al 1999) indicates that even severe flood events on the mainland may be ameliorated by hydrological patterns. Moreover, the moderate salinity flux over the timescales studied here does not seem to be a major concern for those corals that are dominant in nearshore habitats: a small group of robust corals dominated by *Porites* and faviids. The current study indicates that even in conditions where salinity and water quality are carefully maintained at "optimum" levels, larval and juvenile coral survivorship is relatively low; recruitment of sensitive broadcast spawning species such as *A. muricata* is therefore only likely to occur in exceptional years; this is apparently the case in high latitude Pacific and Atlantic coral communities, but was previously thought to be rare in the tropics (Harriott 1999). It is perhaps not surprising that the dominant species in shallow water environments along Thailand's east coast are principally faviid and poritid corals (Kongjandtre 2009) that have here and elsewhere (True *in review*) demonstrated their resistance to moderately severe environments. The historical coral community of an area such as the Gulf of Thailand is thus a mixture of species stratified by their exposure and tolerance of surface salinity flux. In the light of results from the current study, this result may also indicate an extremely long-lived, low-turnover population with infrequent pulses of recruitment.

Unfortunately, ongoing climate change, deforestation and rampant coastal development, together with increased frequency of extreme flood events in the Gulf of Thailand mean that salinity flux is likely to be more widespread and flood events more prolonged in in marginal areas and even those areas not currently exposed to annual flood events. Under the dual impacts of rising seawater temperatures and decreasing water quality, the future coral communities of eastern Thailand are thus likely to be less structurally complex than currently, and to resemble the communities of the inner Gulf. Nearshore reefs in Thailand are likely to be populated by species whose larvae are able to tolerate prolonged hyposalinity and are able to recruit and persist in strongly fluctuating haline environments.

Summary

Reef-building corals are osmoconformers – that is, they do not possess a constant cellular osmolarity, but respond to dynamic changes in their environment. Salinity flux can cause extremely large changes in the cellular chemistry of corals and negatively impact on their relationship with the symbiotic zooxanthellae that supply a large fraction of their energy budget. Corals in near-shore environments are hampered by the already high energetic cost of survival in suboptimal conditions. Although potentially immortal, corals are vulnerable to habitat degradation and environmental impacts that cause stress or damage beyond their ability to repair. Replenishment of coral colonies lost to environmental impacts and natural processes is thus a vital process within coral ecosystems. The replenishment process of coral reefs, however, largely depends on the supply of planktonic larvae, and their ability to settle and grow – particularly in suboptimal conditions. Coastal reefs in South East Asia are under increasing pressure as coastal development reduces shoreline protection and allows greater impacts from terrestrial runoff during wet monsoon seasons. Corals in near-shore environments are thus particularly vulnerable to the effects of climate change in those locations where the coastal landscape has been altered by human activities. This study examined the effects of hyposaline conditions on adult corals of several families, as well as larval survivorship and settlement success to determine whether climate change will compromise the replenishment processes of coral ecosystems in the Gulf of Thailand.

In the first study, we investigated the fertilisation success, larval development and settlement success of 5 species of hard corals from local reef communities exposed to 3 experimental levels of hyposalinity. We found that the rate of development of larvae of the different species was differentially affected by hyposalinity. Larvae of all species under control salinities reached settlement competency in 4-5 days, displaying characteristic behaviors and morphology. In contrast, even moderately reduced salinity caused significant retardation in the rate of larval development across species. Increasingly high levels of deformity and damage were observed with decreasing salinity. Larvae of key habitat-structuring genus *Acropora* were most affected by hyposaline conditions and did not achieve full development under low salinity conditions.

Our results indicate that:
1. heavy rainfall events can exert a strong control on the reproductive success of hard corals, since larval development takes place at the surface of the water column;
2. successful recruitment pulses for many species may only occur in those years where the wet monsoon is delayed, or when river plumes do not affect coastal waters;
3. larval supply is not necessarily the most important factor determining community composition in near-shore coral reefs – since pre- and post-settlement viability can be strongly compromised by even quite minor weather events
4. an increase in coastal runoff due to clearing of vegetation and climate change may remove certain vulnerable species from near-shore reef communities.

In the second study, we used concentration of lipids within coral tissue as a proxy for sublethal stress in corals exposed to different degrees of hyposalinity. We found that nubbins from adult corals exposed to 24 hours of hyposalinity exhibited various behavioural changes associated with stress: e.g. heavy mucus production, cessation of feeding activity. Duration of exposure at moderately low salinities (22-25PSU) appeared to be a critical transition factor for survivorship of the most sensitive species: pulses of low-moderate salinity such as might be associated with severe rainfall events were well-tolerated by the sensitive *Acropora* sp., but prolonged exposure caused rapid declines in lipid reserves and also survivorship. *P.sinensis* and *A. muricata* exhibited apparent changes in tissue lipid concentration due short-duration exposure to lowered salinity. The species most commonly found in the reef flat (and thus exposed to high salinity flux) exhibited little or change in lipid content at the salinities trialled here. The current study indicates that recruitment of sensitive broadcast spawning species such as *Acropora* is only likely to occur in exceptional years. Near-shore areas rich in hyposalinity-averse species are thus likely to be somehow protected from salinity flux. In the light of results from the current study, this result may also indicate that the typical Gulf of Thailand coral community an extremely long-lived, low-turnover population with infrequent pulses of recruitment.

Publications arising from this project:
True JD *(2012)* Salinity as a structuring force for near shore coral communities. [Proc 12th ICRS, Cairns, Australia 2012]
True JD and Piromvaragorn S {*manuscript}* Environmental factors controlling the success of coral reefs in coastal Thailand: salinity as a structuring agent for reef assemblages [target journal: Journal of Coastal Conservation]

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Appendix

Salinity as a structuring force for near shore communities

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Abstract. Corals in near-shore environments are particularly vulnerable to the effects of climate change, especially in those locations where the coastal fluvial landscape has been altered by human activities. The investigation of salinity responses of corals from reefs exposed to river plumes provides insight into the structuring role of monsoonal flooding on coral assemblages and their long-term prognosis. In this study, the effects of hyposalinity exposure on corals acclimated to nearshore conditions were examined for five genera of hard corals. Fertilisation success, larval survivorship and settlement success showed clear trends amongst genera. Unsurprisingly, those species of massive corals that are most common in shallow reef flat environments were the most tolerant of salinity stress as larvae. The most susceptible species were the branching and table Acropora. These trends were repeated in adult corals subjected to prolonged hyposaline conditions. Measurement using tissue lipid concentrations as a proxy for energy reserves reflected the same patterns of stress tolerance. Duration of exposure at moderately low salinities (22-25PSU) was a critical transition factor for survivorship of the most sensitive species: pulses of low-moderate salinity such as might be associated with severe rainfall events were well-tolerated, but prolonged exposure caused rapid declines in lipid reserves and survivorship. These results demonstrate that severe flooding events, such as affected the Gulf of Thailand in 2011 can drastically change the community structure of nearshore reefs and have lasting impacts on the function and replenishment of crucial nearshore habitats.

Key words: coral, community structure, environmental stress, salinity, recruitment.

Introduction

Coastal reefs in South East Asia are under increasing pressure as coastal development reduces shoreline protection and allows greater impacts from terrestrial runoff during wet monsoon seasons. In addition to the increased nutrient input from coastal agriculture, the effects of the terrestrial runoff on coral communities are measured mainly in terms of decreased salinity and input of fine-grained terrigenous sediment (Wilkinson, 1999). As development pressure increases, more coastal forest is cleared and natural barriers to runoff are diminished. Moreover, IPCC models of global climate change in the next century predict that monsoon rainfall in South East Asia will become more intense, exacerbating the vulnerability of coastal coral communities to flood events (Cruz et al 2007).

Corals in stressful environments are hampered by the high energetic cost of survival, whether due to coping with salinity stress, sediment removal or competition (Kleypas et al., 1999). Although potentially immortal, since they are able to replace damaged modules indefinitely, corals are vulnerable to habitat degradation and environmental impacts that cause stress or damage beyond their ability to repair. Moreover, where no existing carbonate platform exists, dissolved calcium carbonate may be present at below saturation levels, thus increasing the cost of carbonate precipitation for the calcifiers (Andersson et al 2007; Kleypas and Yates 2009). When scleractinian corals lose the ability to calcify easily, they are unable to heal damage or to grow, rendering them vulnerable to invasion by pathogens; corals stressed to the point of growth failure certainly do not possess the large energy reserves required for reproduction (Jones and Berkelmans 2011).

Replenishment of coral colonies lost to environmental impacts and natural processes is a vital process within coral ecosystems. In the central south of Peninsular Thailand, a major coral spawning peak occurs around Thai New Year, in March and April – usually just before the onset of the wet monsoon (Piromvaragorn et al., 2006; Kongjandtre et al., 2010). Corals that spawn during this episode risk extreme rainfall events that dramatically reduce surface salinity in coastal areas; thus their replenishment may be

compromised by climatic changes that may increase their exposure to salinity flux. Although there is little extant data on either larval survivorship or settlement success in hyposaline conditions, it is highly likely that the larvae are affected by even short term exposure to salinity stress (Edmonson, 1946).

Reef-building corals are osmoconformers – that is, they do not possess a constant cellular osmolarity, but respond to dynamic changes in their environment, and gain cellular water in hypotonic conditions. All cells require a somewhat stable environment to function optimally; large shifts away from optimum osmolarity can cause changes in macromolecular structure and metabolic function. Therefore, salinity flux can cause extremely large changes in the cellular chemistry of corals and negatively impact on their relationship with the symbiotic zooxanthellae that make it possible for them to construct reef platforms (Mayfield & Gates, 2007). Perhaps more importantly, changes in salinity affect the concentration of ions in the water column, increasing the metabolic cost of calcification in the same way as Ocean Acidification. Indeed, the many of the studies in the past have examined salinity flux only in combination with other stressors (e.g. Hoegh-Guldberg and Smith 1989; Alutoin et al., 2001; Xiubao et al. 2009; Chavanich et al. 2009 {soft corals}), to the extent that ecological effects of changes in salinity are difficult to track.

Most research on the effects of hyposalinity on corals thus far has focussed on the impact of freshwater influx as a short-term stressor, tending to concentrate therefore on the lethality of different degrees of hyposalinity on indicator species. Although this provides valuable insights, it has mostly failed to take account of evidence that coastal coral communities are exposed to seasonal episodes of low salinity and high turbidity resulting from monsoon floods. Bleaching and mortality of near-shore corals and anemones are often reported in association with hypo-saline conditions resulting from heavy rainfall events (e.g. Berkelmans & Oliver 1999; van Woesik et al. 1995). Long-term exposure to hypo-saline conditions on coral reefs is not uncommon, however. For example, decreased salinity levels (28–32 ppt) existed for almost a month after heavy storms on coral reefs located on the Great Barrier Reef (Devlin et al., 1998). During seasonal thunderstorms associated with the onset of the monsoon season, salinity on the reef flat and in the surface layers of the water column can decrease sharply. Salinities measured on the reef flat (average depth ~2m) during one such event at Koh Khai, central Chumphon province, varied from 29PSU at the start of a storm, down to 19PSU after 4 hours of heavy rainfall (pers. obs.). Strong seasonal gradients in salinity resulting from river discharges (e.g. Pearl River, Hong Kong: Morton & Wu, 1975; True,

unpublished) can be quite prolonged, often lasting for several months.

Short-term effects of salinity stress can be exhibited as changes in basal metabolic function, including effects on animal respiration and symbiont photosynthesis. Moberg et al. (1997) reported that two dominant corals on inner Gulf of Thailand reefs (*Porites* and *Pocillopora*) responded quite differently when exposed to sharp changes in salinity, which they attributed to differences in the corals' inherent trophic adaptability. Longer term stress effects can be exhibited as increased mortality rates or reduced growth and reproductive rates (Coles and Jokiel 1992). While significant progress has been made in understanding the effects of altered osmotic conditions on corals, the majority of studies have focused on the effects of hypo-salinity on photosynthesis of the coral's zooxanthellae, or general respiration of coral symbiosis (Muthiga and Szmant 1987; Alutoin et al., 2001; Manzello and Lirman, 2003; Kerswell and Jones 2004), although Downs et al. (2009) demonstrated gross morphological changes in *Stylophora pistillata* in response to prolonged hypo-salinity.

The composition of coral communities is thus a reflection of both the resilience of their constituent species in the face of recurrent prolonged sub-lethal stress, and the vulnerability of species which cannot survive such conditions (but may occur in more benign environments close by). All of Thailand's major coral reefs are fringing types; for the most part they are near the mainland and are thus potentially exposed to strong salinity flux from monsoon rain events and flooding. In this paper, I examine the degree to which salinity might be seen as a proximal structuring force in coastal environments subject to prolonged and profound changes in ocean salinity.

Material and Methods

Experiment 1: In this study, I investigated the fertilisation success, larval development and settlement success of 5 species of hard corals from local reef communities exposed to 3 experimental levels of hyposalinity. Control salinity was ambient Gulf of Thailand inshore levels (32PSU); experimental levels were set at 28 and 24PSU (reported by Moberg et al (1997) to occur for significant periods in the Inner Gulf of Thailand). During a pilot study, it was determined that little additional information was gained from partitioning the study into finer intermediate salinity classes or to pursue extremely low salinities, since 100% mortality of larvae of all species occurred at salinities within 48 hours. In fact, the larvae of no species were able to tolerate prolonged exposure to hyposalinity conditions such as those measured on the reef flat at the time of the experiments (16-19PSU).

Coral gametes were captured as they were released from wild colonies of four common species (*Platygrya sinensis, P. daedalia, Favites abdita and Acropora hyacinthus*) during the annual spawning event at an inshore reef at Ko Mannai, Rayong Province. Gamete bundles were captured from 4-5 colonies of each species. Sperm and eggs were then transferred to 2-litre culture vessels filled with seawater diluted to predetermined experimental salinity levels with sterile fresh water (bottled potable water); 3 replicate vessels were prepared for each species at each salinity. Each culture vessel contained approximately 2000 eggs at the commencement of the experiment. Samples of approximately 40 eggs and/or larvae were pippetted out of the culture vessels at 1-hour intervals for the first 4 hours (when critical developmental changes occur), and then every 12 hours for the first 2 days and every subsequent morning for the remainder of the experiment. Culture vessels were supplied with light aeration and maintained in a shaded environment protected from direct sunlight. Water in the culture vessels was changed for freshly mixed test solutions every 6 hours for the first day, and every 12 hours thereafter. When larvae began to exhibit behavioural changes associated with settlement, pre-conditioned artificial settlement substrates were placed inside the culture vessels.

Rates of deformity and estimated populations in the culture vessels were recorded for each sample. Subsequent to settlement, photographs of settled larvae were made using a Nikon D70 digital camera mounted on a Wild™ stereo microscope. Estimates of numbers of settled larvae made at the same time. Numbers of settled larvae for each species were based on counts from 9 replicates each of circular settlement blocks ~5cm^2; counts included only larvae settled on the upper surfaces.

Experiment 2: To discover the sublethal effects of hyposalinity on adult corals, I exposed samples from 5 colonies of each of five scleractinian coral species (*Acropora muricata, Platygyra sinensis, Pocillopora damicornis, Favites abdita and Turbinaria frondens*) to different degrees of hyposalinity and measured changes in total lipid concentration of their tissues. Samples were obtained from 5m depth in a shallow fringing reef community in Chumphon Province, southern Thailand.

Previous experimentation had indicated that 24 hour exposure to salinities lower than 16PSU were invariably fatal to *Acropora*. In a pilot study, 3 of 5 *Acropora* and 4 of 5 *Pocillopora* nubbins survived 24 hour exposure to 18PSU and subsequent return to ambient salinity, as did 100% of nubbins from the other species. Prolonged exposure to 18PSU salinity (3 days) resulted in 100% mortality for *Acropora* and

Pocillopora, and signs of tissue withdrawal in *Turbinaria* and *Platygyra*. Experimental salinities were therefore fixed to levels that were undoubtedly stressful, but unlikely to be fatal for the subjects over a 24 hour period (i.e. 32 (control), 24 and 18PSU). The experiment was allowed to run for 24 hours, during which observations were made of behavioural (tissue withdrawal or absence of feeding) or gross physical changes (bleaching, tissue sloughing, copious mucus production), after which all samples were removed.

Samples were collected from a coastal reef at a depth of 3m. Six subsamples from each colony were divided into small (~5-6cm^2) pieces and mounted on small concrete pedestals (previously soaked in fresh water for 2 days). Samples were kept in fresh flowing seawater for 1 week to heal before being used in experiments. The experimental apparatus was composed of six identical closed recirculating systems. In each of the recirculating systems, 2100 ml cylindrical plastic containers were connected to upper and lower reservoir tanks. Water was circulated by a 12 volt aquarium pump in the lower reservoir tank, which also contained conditioned aquarium bioballs (for filtration and nitrification). Water was pumped from the lower reservoir tank to the upper reservoir tank at a rate of 20l.sec^{-1}. Gravity-fed water flowed from the upper reservoir and was directed to the bottom of the test chambers by inert silicon tubing. Coral nubbins were assigned to random chambers for each apparatus such that each set had exactly one nubbin from each colony. Water in each experimental unit was changed for fresh seawater once, and 2 hours later changed to target salinity; target salinity was achieved by adding potable water to the lower reservoir of each unit over a period of approximately ½ hour.

Samples were fixed in liquid nitrogen at the completion of the experiment. Surface area of samples was determined using the foil method (Davies 1980); volume of tissue was estimated using either extrapolation (*Acropora*, which has a perforate skeleton – i.e. tissue all the way to the centre of the branch) or from the thickness of the tissue layer (all others). Tissue was removed from the coral skeletons using the Waterpik™ method (Johannes & Wiebe 1970). The resultant aliquot was centrifuged at 3000 rpm for 12 minutes. The supernatant containing the macerated coral tissue was pipette out to a 250ml flask. Total lipid content of the coral tissue was estimated using a gravimetric method (Folch et al, 1957). The total weight of lipid was standardized against estimated tissue volume.

Results and Discussion
The rate of development of larvae of the different species was differentially affected by hyposalinity.

Larvae of all species under control salinities reached settlement competency in 4-5 days, displaying characteristic behaviours and morphology. After the first day's development, few damaged or deformed larvae were observed amongst any species.
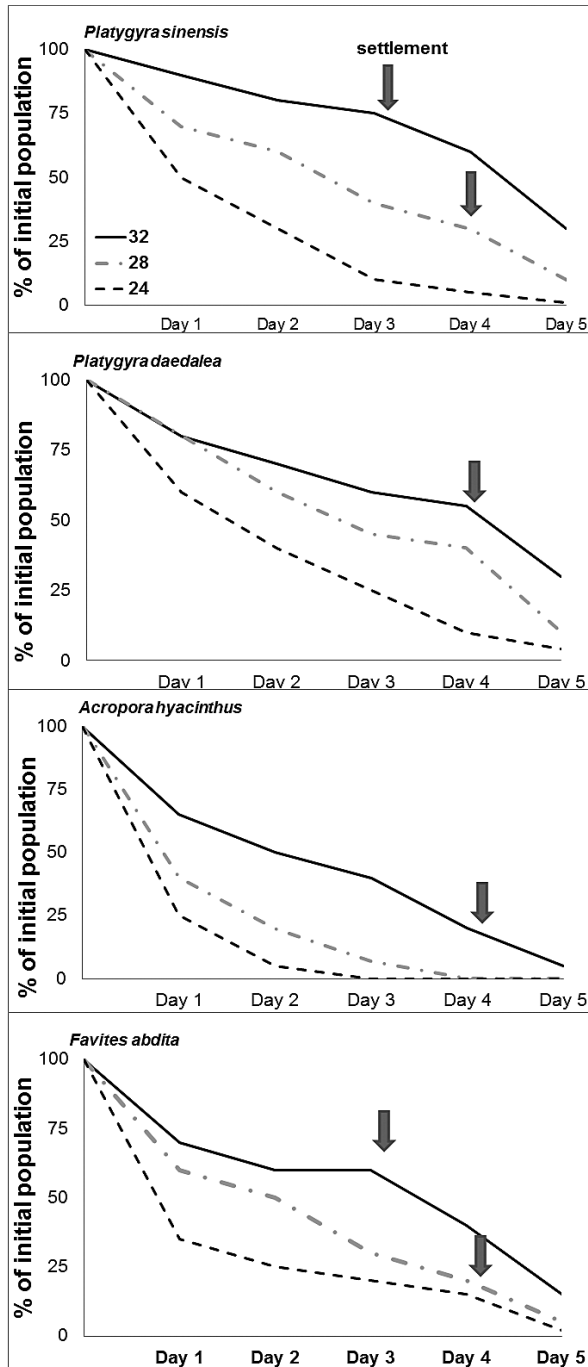

Figure1: Survivorship of coral larvae developing in different salinities; the vertical axis represents the proportion of the initial population (~2000 fertilised eggs) surviving at the end of each day. Arrows indicate settlement events.

In contrast, even moderately reduced salinity caused significant retardation in the rate of larval development across species; moreover, increasingly high levels of deformity and damage were observed with decreasing salinity. Larvae of *Acropora* were most affected by hyposaline conditions and did not achieve full development under low salinity conditions.

Developmental deformity of larvae seemed to be associated with survivorship; initial high levels of larval deformity in the most stressful treatments corresponded with higher mortality. However, there appeared to be no clear relationship between species and rate of deformity (Figure 2).

Mortality amongst larvae in the hyposaline conditions was inversely proportional to salinity and varied amongst species (Figure 1); even a relatively slight reduction in salinity from oceanic standard (35 PSU) as shown by the 32 PSU treatment corresponded to a large reduction in larval survivorship. *Acropora* larvae perished at a much higher rate than did the faviid larvae, to the extent that the populations in the lowest salinity treatments died after only 3 days; while the larvae in the moderate treatment (28PSU) persisted for 4 days, they did not develop to full settlement competency (survivorship to late planula stage dropped to <5% at 28 PSU and zero at lower salinities).

It appears that settlement success of larvae exposed to lower than usual salinities varied between species; those that could be found as adults on the reef flats were able to settle and commence calcification of their exoskeleton even in salinities as low as 24PSU, albeit in much reduced numbers (Table 1). Settlement success of larvae exposed to lower than usual salinities varied between species; those that could be found as adults on the reef flats were able to settle and commence calcification of their exoskeleton even in salinities as low as 24PSU, albeit in reduced numbers and a day later than those at the control salinity.

Table 1: Settlement density of coral larvae reared at different salinities.

Species/Salinity	32PSU	28PSU	24PSU
Acropora hyacinthus	24 $\pm$7	0	0
Favites abdita	150 $\pm$25	70 $\pm$ 21	16 $\pm$ 6
Platygyra daedalea	134$\pm$ 19	41 $\pm$ 16	9 $\pm$7
Platygyra sinensis	118 $\pm$39	51 $\pm$ 15	18 $\pm$ 24

Settled larvae at low salinities were observed to be smaller and paler than the controls, especially amongst the *Platygyra*. Not all settlement blocks in the lowest salinity treatment were successfully settled. Where settlement did not occur in the lower salinity treatments, larvae were observed to have exuded copious amounts of mucus and perished (whether the

mucus production occurred prior to death is unclear: dead cells appeared suddenly, clumped and surrounded by mucus).
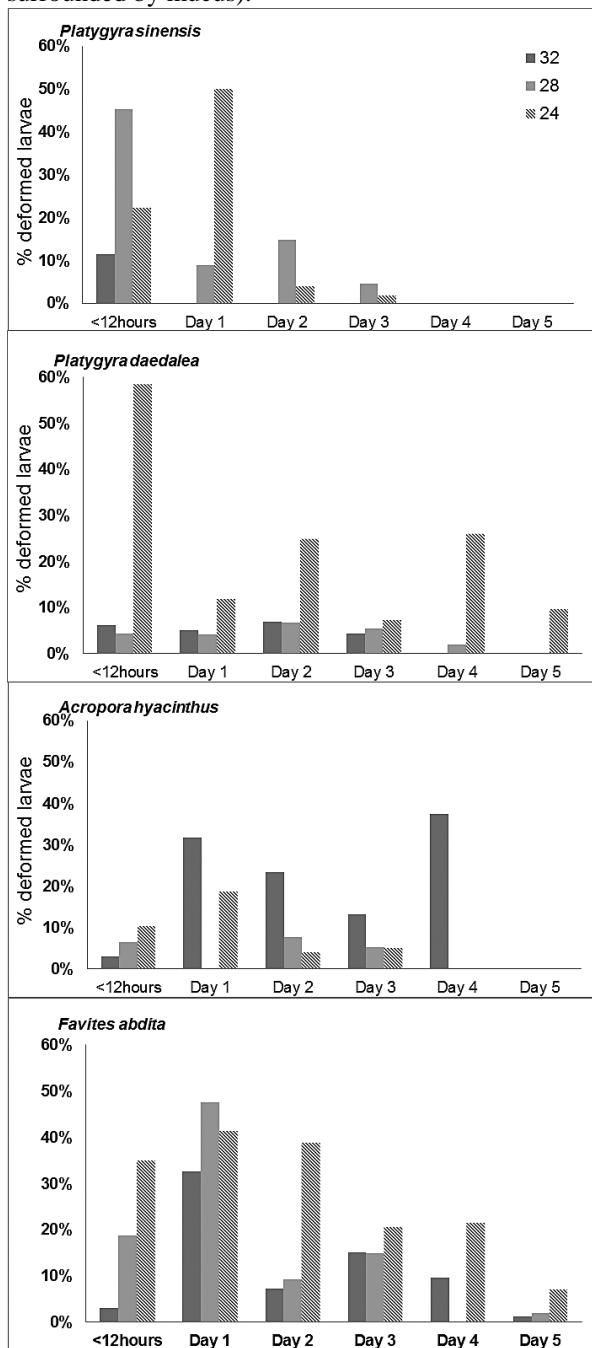

Figure 2: Degree to which hyposalinity appears to have affected development of coral larvae. Some low apparent rates may be due to the rapid breakdown of unviable larvae of some species.

Settlement of larvae of *F. abdita* and *P. sinensis* at lower salinities (28 and 24PSU) appeared to be slightly retarded compared with those in the control salinity; while a few settled larvae were observed on day 3, the majority settled on day 4 (Figure 1). Settled larvae at low salinities appeared to be smaller than the

controls, although it was not possible to measure them with the equipment available.

The replenishment process of coral reefs largely depends on the supply of planktonic larvae. Very little is known about large scale trends in coral reproduction and reproductive success in the Gulf of Thailand. It is known, however, that strong gradients in salinity can seriously compromise reproductive success and recruitment of corals to affected habitats.

Lack of reproductive success and continued replenishment failures can render coral communities vulnerable to extinction even when those communities are composed of robust, flux-tolerant species (True, unpublished). The larvae of broadcast spawning corals do not possess symbiotic zooxanthellae and do not feed whilst in the plankton; larvae must therefore rely on the lipid reserves to settle and create their first skeleton.
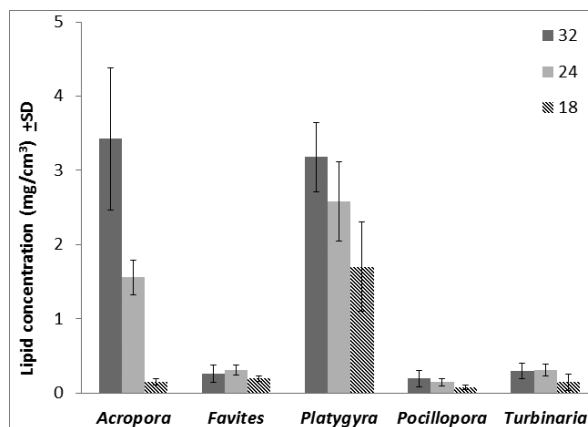

Figure 3: Differences in lipid concentration of coral tissue exposed to hyposalinity.

It is noteworthy, then, that *P.sinensis* and *A. muricata* exhibited apparent changes in tissue lipid concentration due short-duration exposure to lowered salinity (Figure 3), although only the data for *Acropora* were statistically significant. *Acropora* showed significant differences between 32 and 24PSU, and between 24 and 18PSU (1-way ANOVA). No statistically significant difference (1-way ANOVA) in lipid concentration of coral tissue was found between salinity treatments for *P. sinensis, P. damicornis, F. abdita* or *T. frondens* (although *Turbinara* exhibited a difference at α=0.1). In the case of *Platygyra* and *Pocillopora*, this appears to result from the relatively high degree of between-colony variability in lipid concentration. Visual inspection of the data suggests that larger sample sizes may support the statistical validation of apparent biological trends for some of these species. Of the species studied here, only *Favites* and *Platygyra* occur regularly on the reef flat (albeit *Platygyra* prefers the deeper sections of the reef flat) and are thus exposed to strong salinity flux. *A.*

muricata is seldom found inshore in Thailand; its intolerance of even short term hyposalinity appears to offer a good explanation for this.

Nubbins from adult corals exposed to 24 hours of hyposalinity exhibited various behavioural changes associated with stress: e.g. heavy mucus production, cessation of feeding activity. Nubbins at the control salinity exhibited "normal" behaviour for corals in aquariums: polyps and tentacles were extended for prolonged periods and mucus production was minimal. Corals kept at the 24PSU level retracted their polyps and exhibited no signs of activity, but neither did they exude mucus at higher than normal rates. Likewise, corals kept at the lowest (18PSU) salinity exhibited no signs of activity; some mucus was observed in the *Acropora* and *Pocillopora* groups, although output was not continuous. Duration of exposure at moderately low salinities (22-25PSU) thus appears to be a critical transition factor for survivorship of the most sensitive species: pulses of low-moderate salinity such as might be associated with severe rainfall events were well-tolerated by the sensitive *Acropora* sp., but prolonged exposure caused rapid declines in lipid reserves and also survivorship (unpublished data). It is perhaps not surprising that the dominant species in shallow water environments along Thailand's east coast are principally faviid and poritid corals (Kongjandtre 2009) that have here and elsewhere (True unpublished) demonstrated their resistance to moderately severe environments. The historical coral community of an area such as the Gulf of Thailand is thus a mixture of species stratified by their exposure and tolerance of surface salinity flux.

Coral reefs are found only on the eastern side of the Gulf of Thailand (Figure 4). The circulation pattern of the semi-closed Inner Gulf (an anti-clockwise gyre) deflects most of the discharge from the five rivers feeding into the Inner Gulf towards its western margin (Buranapratheprat et al 2002); extensive coral assemblages first become apparent on the western margin of the Gulf at Prachuap Province, some hundred kilometres south of the river plumes. The current and historical community composition of coral reef ecosystems can therefore be used as a strong indication of the types of environmental stresses they are exposed to; rare and exceptional events, such as extreme or prolonged floods, or mass bleaching events may temporarily disturb patterns, but from the results found here, are unlikely to exert strong long-term structuring force on the communities. In the past 2 years (2010-2011), however, Thailand's east coast has been subject to 3 large flood events, the most recent lasting 3 months and transporting an estimated 10 billion cubic meters of water from the Chaopraya watershed into the Inner Gulf of Thailand (2011 AFP). The magnitude and duration of this last event eclipsed

the 2010 mass bleaching event in the scale of its impact on coral reef biota in the Inner Gulf (Yeemin et al 2011). The majority of floodwater flowed SW, creating a prolonged hyposalinity event as far south as Prachuap.
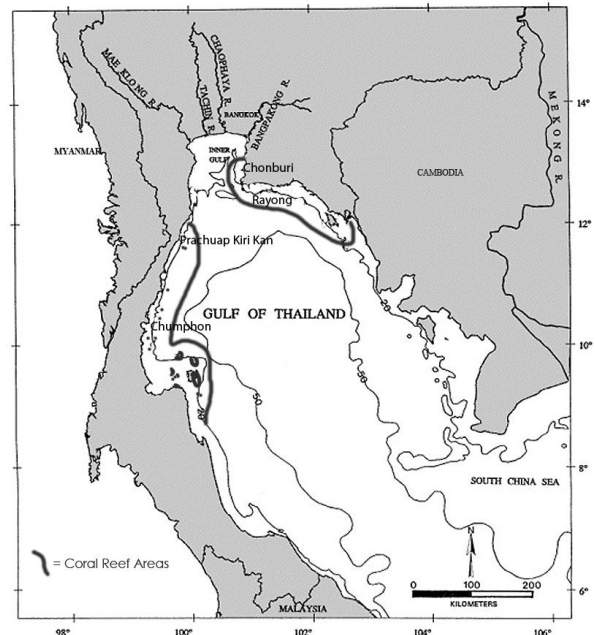

Figure 4: The Gulf of Thailand showing locations described in the text. Reefs occur in from Chonburi east to Cambodia, but are absent along the western margin of the upper Gulf as far south as Prachuap Kiri Kan.

The ubiquitousness of salinity-sensitive species such as *Acropora hyacinthus* in coral assemblages of the eastern Gulf of Thailand (from Chonburi, eastwards: Chansang et al 1999) indicates that even severe flood events on the mainland may be ameliorated by hydrological patterns. Moreover, the moderate salinity flux over the timescales studied here does not seem to be a major concern for those corals that are dominant in nearshore habitats: a small group of robust corals dominated by *Porites* and faviids. There is a rapid increase in coral diversity between Chonburi and Rayong, commensurate with increasingly oceanic water conditions and less exposure to hyposaline pulses. Unfortunately, ongoing climate change, deforestation and rampant coastal development, together with increased frequency of extreme flood events in the Gulf of Thailand mean that salinity flux is likely to be more widespread and flood events more prolonged in in marginal areas and even those areas not currently exposed to annual flood events. Under the dual impacts of rising seawater temperatures and decreasing water quality, the future coral communities of eastern Thailand are thus likely to be less structurally complex than currently, and to resemble the communities of the inner Gulf. Nearshore reefs in Thailand are likely to be populated by species whose

larvae are able to tolerate prolonged hyposalinity and are able to recruit and persist in strongly fluctuating haline environments.

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