Short Contribution

The Transition Zone Chlorophyll Front can Trigger *Acanthaster planci* Outbreaks in the Pacific Ocean: Historical Confirmation

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We hypothesize that the North Pacific transition zone chlorophyll front (TZCF) can episodically deliver enhanced phytoplankton levels that are linked to the emergence of adult populations of the coral eating starfish *Acanthaster planci*. In some years, the seasonally migrating TZCF bathes the northwest Hawaiian Islands with chlorophyll-a rich waters during the winter months that coincide with peak starfish spawning and provide ideal conditions for *A. planci* larval survival. We found significant relationships between starfish populations in the North Pacific and the southernmost latitude of the TZCF, chlorophyll-a concentrations, sea surface temperature, and Ekman transport indices since 1967. We propose that TZCF-triggered primary outbreaks are followed by secondary outbreaks throughout the region, in accordance with the surface currents and separated by a sequential time lag. Our historical confirmation suggests outbreaks are predictable, which has immediate coral reef conservation and management consequences.

1. Introduction

For decades conclusive evidence regarding the cause of *Acanthaster planci* outbreaks has remained elusive. The coral eating starfish are often reported in populations of tens to several hundred thousand (Branham *et al.*, 1971; Goreau *et al.*, 1972; Marsh and Tsuda, 1973), digesting the living tissue off coral colonies (Moran, 1986). Large populations of *Acanthaster planci* have caused extensive coral mortality in the Pacific and Indian Oceans since the late 1960s; for example the Great Barrier Reef in Australia experienced major outbreaks in the 1960's and 1980's, reducing coral cover on many reefs by over 50% (Cameron *et al.*, 1991; Van Woesik, 1994). Similar scenarios have been reported throughout Micronesia and the central Pacific Ocean (Chesher, 1969; Birkeland, 1982).

Experimental work (Ayukai et al., 1997) supports a larval starvation hypothesis proposed by Birkeland

(1982), suggesting that nutrient spikes leading to phytoplankton blooms, for example from watershed runoff, enhance Acanthaster larval survival (Birkeland, 1982; Brodie et al., 2005). High phytoplankton biomass provides the food-limited starfish larvae with the nutrition required to develop from bipinnaria to settling (primordial) larvae. Upon settlement Acanthaster feed on coralline algae and switch their diet to corals after 4–6 months (Yamaguchi, 1973, 1974). Yet, in the last four decades, repeated outbreaks have occurred on many small Pacific islands separated by thousands of kilometers, often simultaneously (Chesher, 1969; Randall, 1972; Marsh and Tsuda, 1973; Birkeland, 1982). Phytoplankton blooms resultant from watershed runoff may potentially enhance Acanthaster survival at the larval stage, but the considerable distance between outbreaks, and their similar frequency suggest a larger scale process may trigger outbreaks in the region.

Alternatively, we provide evidence that a broad oceanographic feature, the transition zone chlorophyll front (TZCF), is primarily responsible for delivering the en-

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Fig. 1. Map of the study region showing the proposed Acanthaster outbreak cycle (grey arrow).



Fig. 2. Comparison of SeaWiFS surface chlorophyll-a (mg/m³) data for a geographic box around Hawaii (22°-28°N, 178°-160°W) during an *Acanthaster* non-outbreak (2001) and outbreak year (2005), respectively.



Fig. 3. Significant relationship found between the winter, lowest latitude of the .15 mg/m³ average monthly chlorophyll-a contour (considered an anomaly for this region) in a geographic box around the Hawaiian Islands (22°– 28°N, 178°–160°W), and annually averaged Acanthaster abundances on Commonwealth of the Northern Mariana Islands reefs from 2000–2005.

hanced phytoplankton levels ideal for starfish spawning (e.g. the emergence of fecund adults) and larval survival in the northwest Hawaiian Islands. The TZCF separates nutrient-rich subpolar waters from oligotrophic subtropical waters across the North Pacific Ocean basin (Polovina et al., 2001). We hypothesize that the annual, southward migrations (winter-time low positions) of the TZCF (Bograd et al., 2004) represent the southerly displacement of phytoplankton rich waters, and trigger primary Acanthaster outbreaks. This is consistent with the reproductive biology of the starfish, which shows peak fertility during the winter months in the North Pacific Ocean (Branham et al., 1971; P. Houk, pers. obs.). We further posit that primary outbreaks in Hawaii are followed by secondary outbreaks throughout the north Pacific Ocean (Fig. 1). We do not propose that the TZCF is responsible for the secondary outbreaks, but rather that these are a consequence of the prevailing ocean surface currents and the islands' geographic locality. Here we use historical data to test our theory. A second example is then presented to support the idea that oceanically derived phytoplankton rich waters, other than the TZCF, acted in a similar fashion to produce an Acanthaster outbreak in Palau in 1998.

2. Relationships between Large-Scale Oceanographic Processes and Acanthaster planci Populations

Depending on the position of the TZCF, relatively high chlorophyll concentrations can bathe the northwest Hawaiian Islands during winter months (Fig. 2). Data from



Fig. 4. Relationships between temperature, Ekman transport, and SeaWiFs derived chlorophyll-a concentrations during the winter months (December–February) of 1997–2004 averaged for a geographic box around the Hawaiian Islands (22°–28°N, 178°–160°W).

the Sea-viewing Wide Field-of-view Sensor (SeaWiFs) show that unusually high chlorophyll concentrations existed throughout the northwest Hawaiian Islands during the 2004–5 winter as compared with a typical year (Fig. 2). The presence of phytoplankton rich waters was followed by Acanthaster outbreak populations on Johnston Atoll (Brainard et al., 2005), and by sequential outbreaks in the Marshall (Pinca et al., 2005) and Southern Mariana Islands (P. Houk, pers. obs.), separated by a ~2 month time lag (Fig. 1). We propose that phytoplankton rich waters associated with the TZCF triggered primary outbreaks in Hawaii, and use historical outbreak data to test our theory (below). Further, we suggest that North Pacific surface currents (Bonjean and Lagerloef, 2002) link the TZCF-triggered primary outbreaks in the Hawaiian Islands with the secondary populations at Johnston Atoll, the Marshall, and the Mariana Islands (Fig. 1). Surface currents associated with the North Pacific Gyre reportedly follow this trajectory, especially during the winter months (Eldredge, 1983; Bonjean and Lagerloef, 2002; http://www.oscar.noaa.gov/datadisplay/index.html). Hydrodynamic based larval transport models and present day distributions of coral and gastropod fauna indicate a corridor for larval transport between Johnston Atoll, the NW Hawaiian, main Hawaiian, Marshall, and Mariana Islands (Vermeij et al., 1983; Randall, 1995; Maragos et al., 2004; Kobayashi, 2006). In support, we found a significant relationship between adult Acanthaster populations in the Mariana Islands and the southernmost latitude of the TZCF in the NW Hawaiian Islands over the past 6 years (Fig. 3). Nevertheless, the mechanism driving the secondary outbreaks is unknown.

3. Migration of the Transition Zone Chlorophyll Front

The TZCF is a zone of surface convergence where cool, high-chlorophyll surface waters from the north sink beneath warm, oligotrophic waters to the south (Polovina



Fig. 5. Minimum winter (December–February) sea surface temperature and meridional Ekman Transport indices from 1967–2005 for a geographic box around the Hawaiian Islands ($22^{\circ}-28^{\circ}N$, $178^{\circ}-160^{\circ}W$). Large numbers represent reported outbreak years (Table 1); (*) Represents the documentation of non-outbreak starfish populations (Marsh and Tsuda, 1973; Randall, 1991; Quinn and Kojis, 2003, respectively). There is a significant relationship between historical *Acanthaster* outbreaks (Table 1) and Ekman Transport indices (p = 0.003, logit regression).

et al., 2001). SeaWiFs data show the TZCF migrating seasonally from 40–45°N in the summer to 30–35°N in the winter (Polovina et al., 2001), with significant interannual variability (Bograd et al., 2004). Simple models have shown that the latitudinal variation of the TZCF depends upon the amount of light and inorganic nutrients available for primary production, at a given latitude, and the extent of vertical mixing (Glover et al., 1994; Chai et al., 2003). Interannual variability in the magnitude of Ekman pumping and horizontal divergence driven by the wind stress curl also determine the southerly extent of the wintertime TZCF (Bograd et al., 2004). Cooler sea surface temperatures and strong equator-ward Ekman transport are indicative of a more southerly displacement of the TZCF, which can occasionally extend to the Hawaiian Islands. Our results indicate that average monthly sea

Table 1. Location and citation data for *Acanthaster* outbreaks noted in Fig. 5.

Event on graph	Island	Citation
1 (1969–70)	Hawaii	Branham <i>et al.</i> , 1971
1 (late 1960's)	Marshall Islands	Pinca <i>et al.</i> , 2005
1 (1967–69)	Mariana Islands	Chesher, 1969
2 (1979–81)	Mariana Islands	Birkeland, 1982
3 (1985–86)	Mariana Islands	Randall <i>et al.</i> , 1988
4 (2003–05)	Johnston Atoll	Brainard <i>et al.</i> , 2005
4 (2003–05)	Marshall Islands	Pinca <i>et al.</i> , 2005
4 (2003–05)	Mariana Islands	P. Houk, pers. obs.



Fig. 6. Surface chlorophyll-a concentrations (mg/m³) in the northwestern Pacific, including Palau, during an *Acanthaster* outbreak year (1998) and non-outbreak years (2004, 2005).

surface temperatures and meridional Ekman transport explained 71% and 65% of the variance in surface chlorophyll-a concentrations, respectively, in a geographic box around the NW Hawaiian islands (178°–160°W, 22°– 28°N) (Fig. 4). The relationships suggest that Ekman transport and sea surface temperature data, both available from 1967–present, can be used as a proxy of historical chlorophyll concentrations (Fig. 5).

Relationships found between oceanographic conditions and Acanthaster outbreaks suggest that their populations are predictable and our hypotheses are testable. Here, we utilize historical sea surface temperature and meridional Ekman transport data for a geographic region surrounding the Hawaiian Islands from 1967 to the present; we compared predicted outbreak years with those reported in the literature (Fig. 5, Table 1). Between 1967–2005, Acanthaster outbreaks in the Mariana Islands, the Marshall Islands, Johnston Atoll, and the Hawaiian Islands were significantly related to Ekman transport indices (p = 0.003, logit regression). Notably, the largest negative Ekman transport occurred in 1968, coinciding with the first (reported) and largest starfish outbreak on Guam reefs (Chesher, 1969). During the following year, observations on the Hawaiian reefs found persistent populations remaining (Branham et al., 1971). Historical data support a strong coupling between high phytoplankton biomass and Acanthaster outbreaks. However, outbreak populations frequently persist for up to 2.5 years after initiation (Chesher, 1969; Branham et al., 1971), which are largely dependent upon coral cover (i.e., food availability).

4. Evidence from Palau

We further tested our hypothesis in Micronesia. A review of SeaWiFs data shows a migrating chlorophyll front, not related to the TZCF, of varying magnitude and direction from Indonesia north to Palau, during winter and early spring (Fig. 6). This feature originates from the North Equatorial Counter-Current and the Mindanao Eddy which influence Palau from December–April (Heron *et al.*, 2006). An *Acanthaster* outbreak was evident during the 1998 El Niño Southern Oscillation (Bruno *et al.*, 2001; P. Houk, pers. obs.), concurrent with the migration of a large chlorophyll front over Palau (Fig. 6). This second example advances our hypothesis that the transport of productive waters to coral reefs is one of the primary causes of *Acanthaster* outbreaks in the North Pacific.

5. Discussion and Summary

The direct relationship between adult populations and high chlorophyll-a concentrations is perplexing, however, particularly since settling larvae take ~3 years to reach adulthood (Yamaguchi, 1973; Zann *et al.*, 1987; Birkeland, 1989). The present data suggest a much shorter development period, or, more likely, that cooler, chlorophyll-rich waters are acting directly upon the adult starfish.

Phytoplankton biomass associated with the migrating TZCF is sufficient to drive ecological food webs and explain spatial distributions of several fish and mammal populations (Polovina *et al.*, 2001). Here, we suggest that high phytoplankton densities favor the emergence of fecund *Acanthaster* adults that spawn, allowing for a high survival of larvae. In support we found that chlorophyll-a concentrations are significantly positively related to adult *Acanthaster planci* populations. We also suggest that the near-surface circulation within the North Pacific Ocean most likely provides connectivity among primary and secondary *Acanthaster* populations.

Our findings have immediate consequences for many facets of North Pacific Ocean coral reef ecology. First, real-time satellite imagery can facilitate the prediction of *A. planci* outbreaks, much like ocean warming and coral bleaching events. Second, armed with predictive capacity, a removal program may be a viable option for many small island nations with limited management budgets and a desire to protect economically important reefs. Finally, our results can stimulate investigations into coral community dynamics, providing an influential predictor of past and future disturbances.

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References

- Ayukai, T., K. Okaji and J. S. Lucas (1997): Food limitation in the growth and development of Crown-of-Thorns starfish larvae in the Great Barrier reef. *Proc. 8th Int. Coral Reef Symp.*, 1, 621–626.
- Birkeland, C. (1982): Terrestrial runoff as a cause of outbreaks of Acanthaster planci (Echinodermata: Asteroidea). Mar. Biol., 69, 175–185.
- Birkeland, C. (1989): The Faustian traits of Crown-of-Thorn starfish. Am. Sci., 77, 154–163.
- Bograd, S. J., D. G. Foley, F. B. Schwing, C. Wilson, R. M.

Laurs, J. J. Polovina, E. A. Howell and R. E. Brainard (2004): On the seasonal and interannual migrations of the transition zone chlorophyll front. *Geophys. Res. Lett.*, **31**, L17204.

- Bonjean, F. and G. S. E. Lagerloef (2002): Diagnostic model and analysis of the surface currents in the tropical Pacific Ocean. J. Phys. Oceanogr., **32**, 2938–2954.
- Brainard, R., J. Maragos, R. Schroeder, J. Kenyon, P. Vroom, S. Godwin, R. Hoeke, G. Aeby, R. Moffitt, M. Lammers, J. Gove, M. Timmers, S. Holzwarth and S. Kolinski (2005): The state of coral reef ecosystems of the U.S. Pacific remote island areas. p. 338–372. In *The State of Coral Reef Ecosystems of the Unites States and Pacific Freely Associated States*, ed. by J. Waddell, NOAA Technical Memorandum NOS NCCOS 11, Silver Spring, Maryland.
- Branham, J. M., S. A. Reed, J. H. Bailey and J. Caperon (1971): Coral-eating sea stars *Acanthaster planci* in Hawaii. *Science*, **172**, 1155–1157.
- Brodie, J., K. Fabricius, G. De'ath and K. Okaji (2005): Are increased nutrient inputs responsible for more outbreaks of Crown-of-Thorn starfish? An appraisal of the evidence. *Mar. Poll. Bull.*, **51**, 266–278.
- Bruno, J. F., C. E. Siddon, J. D. Witman, P. L. Colin and M. A. Toscano (2001): El Niño related coral bleaching in Palau, western Caroline islands. *Coral Reefs*, **20**, 127–136.
- Cameron, A. M., R. Endean and L. M. DeVantier (1991): Predation on massive corals: Are devastating population outbreaks of *Acanthaster planci* novel events? *Mar. Ecol. Prog. Ser.*, **75**, 251–258.
- Chai, F., M. Jiang, R. T. Barber, R. C. Dugdale and Y. Chao (2003): Interdecadal variation of the transition zone chlorophyll front, a physical-biological model simulation between 1960 and 1990. J. Oceanogr., 59, 461–475.
- Chesher, R. H. (1969): Destruction of Pacific corals by the sea star Acanthaster planci. Science, **165**, 280–283.
- Eldredge, L. G. (1983): Summary of environmental and fishing information on Guam and the Commonwealth of the Northern Mariana Islands: historical background, description of the islands, and review of the climate, oceanography, and submarine topography. NOAA Technical Memorandum NMFS-SWFC-40, United States Department of Commerce.
- Glover, D. M., J. S. Wroblewski and C. R. McClain (1994): Dynamics of the transition zone in coastal zone color scanner-sensed ocean color in the North Pacific during oceanographic spring. J. Geophys. Res., 99, 7501–7511.
- Goreau, T. F., J. C. Lang, E. A. Graham and P. D. Goreau (1972): Structure and ecology of the Saipan reefs in relation to Acanthaster planci (Linnaeus). Bull. Mar. Sci., 22, 113–152.
- Heron, S. F., E. J. Metzger and W. J. Skirving (2006): Seasonal variations of the ocean surface circulation in the vicinity of Palau. *J. Oceanogr.*, **62**, 413–426.
- Kobayashi, D. R. (2006): Colonization of the Hawaiian archipelago via Johnston Atoll: A characterization of oceanographic transport corridors for pelagic larvae using compu-

ter simulation. Coral Reefs, 25, 407-417.

- Maragos, J. E., D. C. Potts, G. Aeby, D. Gulko, J. Kenyon, D. Siciliano and D. Van Ravenswaay (2004): 2000–2002 rapid ecological assessment of corals (Anthozoa) on shallow reefs of the northwestern Hawaiian islands. Part I: species and distribution. *Pac. Sci.*, **58**, 211–230.
- Marsh, J. A. and R. T. Tsuda (1973): Population levels of *Acanthaster planci* in the Mariana and Caroline Islands. *Micronesica*, **9**, 165.
- Moran, P. J. (1986): The Acanthaster phenomenon. Oceanogr. Mar. Biol. Annu. Rev., 24, 379–480.
- Pinca, S., M. Beger, D. Jacobson and T. Keju (2005): The state of coral reef ecosystems of the Marshall Islands. p. 373–386. In *The State of Coral Reef Ecosystems of the Unites States and Pacific Freely Associated States*, ed. by J. Waddell, NOAA Technical Memorandum NOS NCCOS 11, Silver Spring, Maryland.
- Polovina, J. J., E. Howell, D. R. Kobayashi and M. P. Seki (2001): The transition zone chlorophyll front, a dynamic global feature defining migration and foraging habitat for marine resources. *Prog. Oceanogr.*, **49**, 469–483.
- Quinn, N. J. and B. L. Kojis (2003): The dynamics of coral reef community structure and recruitment patterns around Rota, Saipan, and Tinian, western Pacific. *Bull. Mar. Sci.*, **72**, 979– 996.
- Randall, J. E. (1972): Chemical pollution in the sea and the Crown-of-Thorns starfish. *Biotropica*, **4**, 132–144.
- Randall, R. H. (1988): A Marine Survey of the Obyan-Naftan Reef Area. University of Guam Tech. Rep. 90, Mangilao, Guam.
- Randall, R. H. (1991): Community Structure of the Corals along the Fringing Reefs Bordering Unai LauLau Kattan, Unai Baput, and Unai LaoLao Beaches in Saipan, CNMI. Cheenis Pacific Co., Saipan, CNMI.
- Randall, R. H. (1995): Biogeography of reef-building corals in the Mariana and Palau Islands in relation to back-arc rifting and the formation of the Eastern Philippine Sea. *Nat. Hist. Res.*, **3**, 193–210.
- Van Woesik, R. (1994): Contemporary disturbances to coral communities of the Great Barrier Reef. J. Coast. Res., 12, 233–252.
- Vermeij, G. J., E. A. Kay and L. G. Eldredge (1983): Molluscs of the northern Mariana Islands, with special reference to the selectivity of oceanic dispersal barriers. *Micronesica*, 19, 27–55.
- Yamaguchi, M. (1973): Early life history of coral reef asteroids, with special reference to Acanthaster planci (L.).
 p. 369–387. In *Biology and Geology of Coral Reefs*, ed. by O. A. Jones and R. Endean, Academic Press, New York.
- Yamaguchi, M. (1974): Growth of *Acanthaster planci* (L.) in the laboratory. *Pac. Sci.*, **28**, 123–138.
- Zann, L., J. Brodie, C. Berryman and M. Naqasima (1987): Recruitment, ecology, growth and behaviour of juvenile *Acanthaster planci* (L.) (Echinodermata: Asteroidea). *Bull Mar Sci*, 41, 561–575.