



CONTENTS

Words from the Chair

SCRFA Update

CARIBBEAN & ATLANTIC
United States

INDO-PACIFIC
Australia
Palau

Perspectives

New Publications



© C. Parsons



© J. Lam (original photos: S. Shea)



© D. Cook

BREAKING NEWS

First-ever! Camouflage grouper spawning aggregations observed and documented in Palau

Snapper-grouper fisheries in the US South Atlantic: more spatial management measures underway

Call for sustainability: An update of a grey mackerel fishery in Australia

For more information, see Newsletter



WORDS

from the chair

The SCRFA Board of Directors has recently changed. I would like to thank Janet Gibson (Belize), Pat Colin (Palau) and Terry Donaldson (Guam) for their great work and support in helping to make SCRFA the organisation it now is. They have retired from the Board, making way for three new Board members, launching SCRFA into a new and exciting phase of development, work and influence. The next Board meeting will be in October this year.

The SCRFA Board now comprises the following people working on fish spawning aggregations in our key focus areas of scientific research, education and management of reef fish spawning aggregations: Martin Russell (Australia); Yvonne Sadovy (University of Hong Kong); Michael Domeier (Marine Conservation Science Institute, USA); Brian Luckhurst (retired Bermuda Fisheries Scientist, Italy); Sebastian Troeng (Conservation International, USA); Brad Erisman, (Scripps University, USA); Rick Nemeth (University of the Virgin Islands); and Rick Hamilton (The Nature Conservancy, Australia). Please visit our website for more 'about us' [<http://www.scrfa.org/index.php/about-us.html>].

The new Board will help further develop SCRFA's focus on working together with countries, especially where coastal communities depend heavily on reef fisheries, on their fish spawning aggregations, and facilitating sustainable coral reef fish fisheries of which aggregation management is a key part. We have come a long way since our humble beginning in 2000 at the American Society of Ichthyologists and Herpetologists meeting in Mexico. In addition to education and research projects, our core aim is to have spawning aggregations routinely considered in national and international management and conservation forums and planning initiatives.

Martin Russell
Chair/CEO
SCRFA

SCRFA

update

Once again I am in Fiji working on a project we have been doing with the Fiji Fishery Research Office on a spawning aggregation located in a small marine protected area (MPA) off the island of Kadavu, south of Fiji's capital, Suva. I have just learned that several of the fish we tagged in the Naiqoro Channel in July/August 2009 have been recaptured, and was fortunate to meet the fisher who caught them (see photo). Fiji is one of our focal study areas and we have been working here since the early 2000s, conducting fisher interviews and field work. At Naiqoro passage we are doing a baseline survey of the grouper aggregation site, one of the best known in Fiji.



© William Donaldson

*Yvonne giving the fisherman Freddy Turaga from Lagalevu village in Kadavu, Fiji a T-shirt reward for returning tags from *Epinephelus polyphekadion*.*

*Fish were tagged in July/August 2009
The furthest fish was found 15 km from the tagging site in May 2010*

Our other focal area currently is Palau, where we have just finished 18 months of field studies in an MPA in Ebiil Channel building on our initial work doing fisher interviews in 2003 [<http://www.scrfa.org/index.php/case-studies/palau.html>]. We have been working with the Palau Conservation Society on educational projects related to the field study.

Looking back over these and other projects and our 10-year engagement with aggregation conservation and management, important lessons learned are that building long-term personal links and relationships is very important for being effective, and that there is still a real need to focus strongly on reef fish fisheries as a whole, while fostering an understanding of the role of aggregations within them. With this in mind, SCRFA is currently producing a film on Palau's coastal fishery and is also part of a newly formed fishery/MPA working group within ICRI (International Coral Reef Initiative), following a meeting in Monaco earlier this year. At this meeting it was very clear that much more attention is needed for coastal reef fishery management in general, over and above the protection of the coral reef habitats themselves and the use of MPAs. We will follow up on this at the next ICRI meeting in November this year in Samoa.

Finally, I would like to draw your attention to our Blog on the SCRFA website, [<http://fishspawning.wordpress.com/>]. Please check this from time to time and consider commenting on issues of interest to you - there is much we can learn from exchanging information with each other as interest in marine issues rapidly grows.

Yvonne Sadovy
Director, SCRFA
yjsadovy@hku.hk

U.S.A.

South Atlantic Fishery Management Council Approves Measures to Address Overfishing Snapper-Grouper Species (see also Newsletter 13)

The South Atlantic Fishery Management Council (SAFMC) is responsible for the conservation and management of fish stocks within its jurisdiction through the development of fishery plans, with requirements to prevent and stop overfishing, minimize bycatch, and protect habitat. In our last Newsletter (No. 13) we suggested that spatial measures could also be applied. In feedback to that article, we were advised that there is already some spatial protection involved, and that efforts are now being made to incorporate more spatial measures in management planning in the snapper-grouper fishery of the region.

While multiple conventional fishery management measures are applied to several of the fisheries under SAFMC jurisdiction, it is only more recently that spatial measures have begun to specifically address spawning aggregation sites. This is partly due to the fact that, despite several species being confirmed aggregation spawners, their aggregation sites are generally not widely known outside the fishing community, while spawning seasonality is better understood, facilitating the seasonal protective measures currently in place for a number of species during their reproductive periods.



Plan for the proposed snapper-grouper area closure
Map extracted from SAFMC

[<http://www.safmc.net/News/NewsReleases/NR-June182010/tabid/647/Default.aspxSAFMC>]

In December 2009, the SAFMC approved amendment 16 of the Fishery Management Plan for the snapper-grouper fishery in the region [<http://www.safmc.net/Portals/6/Library/FMP/SnapGroup/SnapGroupAmend16FINAL.pdf>]. This amendment addresses overfishing for nine snapper and grouper species (golden tilefish *Lopholatilus chamaeleonticeps*, snowy grouper *Epinephelus niveatus*, speckled hind *E. drummondhayi*, Warsaw grouper *E. nigritus*, black grouper *Mycteroperca bonaci*, black sea bass *Centropristis striata*, gag *M. microlepis*, red grouper *E. morio*, and vermilion snapper *Rhomboplites aurorubens*), most of them aggregation-spawners, by establishing annual catch limits and introducing accountability measures.

Amongst other measures, this amendment involves spatial deepwater closures (73 m seaward) for deepwater species to help protect Warsaw grouper and speckled hind, two fishes extremely vulnerable to overfishing and for which no landings are permitted either commercially or recreationally. The deepwater closure is expected to also help protect other deepwater species (snowy grouper, blueline tilefish *Caulolatilus microps*, yellowedge grouper *E. flavolimbatus*, misty grouper *E. mystacinus*, queen snapper *Etelis oculatus* and silk snapper *Lutjanus vivanus*) where fishing, possession, and retention of these species are prohibited. As knowledge increases on the spawning locations, their seasonal or year-round protection can be applied as a management measure, especially the species included in this management plan that are of conservation concern [www.iucnredlist.org] and are verified aggregation-spawners (Sedberry *et al.* 2006).

A new amendment (17A), recommended by the SAFMC, suggests to extend the red snapper closure and a large area closure (~17,000 square km) in waters from 30 m to 73 m where fishing, except for spearfishing and use of black sea bass pots, for all snapper and grouper species would be prohibited to address overfishing, as well as to reduce the high mortality associated with discards. This amendment, alongside the newly designated Coral Habitat Areas of Particular Concern encompassing ~60,000 square km, will hopefully protect important spawning habitats that fall within the boundary.

Summarized by Joy TL Lam
SCRFA
tllam.joy@gmail.com

Reference: Sedberry G.R., O. Pashuk, D.M. Wyanski, J.A. Stephen, P. Weinbach (2006) Spawning locations for Atlantic reef fishes off the southeastern U.S.. 57th Gulf and Caribbean Fisheries Institute, 464-514

Protecting Mutton Spawning Aggregations in the Dry Tortugas

References:

Aguilar-Perer A. (2006) Disappearance of a Nassau grouper spawning aggregation off the southern Mexican Caribbean coast. *Marine Ecology Progress Series*, 327: 289 – 296.

Burton M.L., K.J. Brennan, R. C. Muñoz, R.O. Parker Jr. (2005) Preliminary evidence of increased spawning aggregations of mutton snapper (*Lutjanus analis*) at Riley's Hump two years after establishment of the Tortugas South Ecological Reserve. *Fisheries Bulletin*, 103: 404-410.

Domeiere M.L. (2004) A potential larval recruitment pathway originating from a Florida marine protected area. *Fisheries Oceanography*, 13: 287 – 294.

Domeier M.L., Koenig, C. & Coleman, F. (1996) Reproductive biology of gray snapper (*Lutjanus griseus*) with notes on spawning for other western Atlantic snappers (Lutjanidae). In: *Biology and culture of tropical groupers and snappers*. F. Arreguin-Sanchez *et al.*, (eds), p 189 – 201. ICLARM Conference Proceedings 48, Makati City, Philippines.

Heyman W.D., B. Kjerfve (2008) Characterization of transient multi-species reef fish spawning aggregations at Gladden Spit, Belize. *Bulletin of Marine Science*, 83: 531-551.

Lindeman K.C., R. Pugliese, G.T. Waugh, J. S. Ault (2000) Developmental patterns within a multispecies reef fishery: management applications for essential fish habitats and protected areas. *Bulletin of Marine Science*, 66: 929-956.

The mutton snapper, *Lutjanus analis*, migrates to specific sites to form annual transient spawning aggregations in the tropical western Atlantic (Domeier *et al.* 1996; Lindeman *et al.* 2000; Heyman and Kjerfve 2008). Regrettably, previous fishery management strategies have not always considered the susceptible nature of reef fish spawning aggregations (FSAs), allowing them to be rapidly depleted by unregulated fishing activities (Aguilar-Perera 2006). In 2001 the Tortugas South Ecological Reserve (TSER) was established to alleviate pressure on a historical mutton spawning aggregation site. This area is considered a critical source of recruits to southeast Florida and the Florida Keys (Domeier 2004). Re-formation of the mutton spawning aggregation has been documented since the closure of the TSER (Burton *et al.* 2005) but little is known about adult fish movements within the Dry Tortugas region.

In May 2008, a study was initiated by Florida Fish and Wildlife Conservation Commission's Fish and Wildlife Research Institute (FWC) to determine movement patterns and spatial range of adult mutton snapper using telemetry. An array of 64 acoustic receivers was deployed throughout the Dry Tortugas region. This array covers approximately 800 square km² and is designed to measure both small-scale movement and long-range migrations of tagged mutton snapper through a variety of benthic habitats. To date, 48 mutton snappers have been surgically implanted with coded transmitters (Fig. 1). Some individuals have been documented making repeated migratory round trips of up to 50 km to the spawning grounds during the spawning season (maximum of 4 trips per individual). The greatest distance recorded, to date, of a tagged fish away from the aggregation site is 55 km. Preliminary results also indicate that FSA residency times by individual fish may span up to 16 days around the full moon from May to August.



Fig. 1 FWC research scientists perform surgery underwater to acoustically tag a mutton snapper.

Thousands of mutton snapper are estimated to be present on the spawning grounds around the full moon, although smaller subgroups of 20 – 60 fish will break away from the main FSA during a spawning event. For the first time in Florida, subgroups of mutton snapper were observed spawning within the TSER in the late afternoon, 5 days after the full moon (see cover, top figure, a subgroup of mutton snapper spawning in Florida).

Information from this study will help establish the degree of connectivity between different management areas of the Dry Tortugas and determine the efficacy of those management areas for providing adequate habitat to encompass home ranges and migratory pathways of reef fish species. Future work will expand to other ecologically and economically valuable species, such as black grouper, *Mycteroperca bonaci*, that may also utilize this and possibly other sites yet to be discovered.

Danielle Morley
Florida Fish and Wildlife Conservation Commission
Danielle.Morley@MyFWC.com

AUSTRALIA

INDO-PACIFIC

Study on Coral Reef Fish Spawning Closures Help Formulate Adaptive Management in Australia

A review of annual coral reef fish fishery spawning closures in Queensland, Australia was conducted by the Fishing and Fisheries Research Centre of James Cook University in 2008, four years after implementation, to determine the effectiveness of the closures. Designed to protect reef fish from fishing during spawning throughout the entire Great Barrier Reef (GBR), the spawning closures covered the three new moon periods from October to December, for 9 days each from 2004 to 2008, inclusive. The closures were planned around the reproductive timing of coral trout, *Plectropomus leopardus*, the dominant reef fish species in the GBR commercial catch, but with consideration for other exploited reef fish species.

Available information on the spawning activity of the main target species and how this relates to the three 9-day closures regime as well as economic and social impacts of current and alternative spawning closures on commercial, recreational and charter fishers were examined. While there were few biological or monitoring data, the findings suggested that the closures provide some protection at the time of spawning of most of the important species in the fishery, including groupers and to some extent snappers and emperors. However, there was a significant difference in the effectiveness of each of the closures as judged by their timing. A closure in October has the highest potential to protect spawning fish. Meanwhile, December saw only an effect similar to the unprotected January and June calculated under the closure effectiveness index - taken into account the number of species that spawn in the given closure month plus the proportion each of those species makes up of the catch in a given month and in the fishery overall.

The possible economic and social consequences associated with the three 9-day closures were estimated by calculating lost revenue in 2007 according to the available coral trout quota and average beach price for the year. Commercial line fishers experienced a 13% loss of potential coral trout revenue for the three 9-day closures at the time of the survey. Costs of alternative closures were also calculated: for instance there was a loss of 8% coral trout revenue for two 9-day closures in November and December, and an estimated 0.5% loss for two 5-day closures in October and November from the coral trout fishery (a reduction in cost of 97%). Applying similar calculations to the charter fishery based on revenue per 'lost' fishing day suggested a loss

of 13% of their potential revenue. Fisher interviews conducted in 2008 indicated the closures imposed social and economic hardships on commercial line fishers and charter fishers. These two fishery sectors regarded closures negatively, while aquarium fishers and seafood processors thought the contrary, while acknowledging a negative financial effect on their business. Most fishers considered that the costs of closures outweighed any potential benefits to the reef fishes affected, seeing this measure as unnecessary because there are other management tools already in place that help towards managing the species concerned, (e.g. marine park zoning, size limits, commercial quotas, recreational bag limits).



© Jan Messersmith

Coral trout, *Plectropomus leopardus*

The scientists involved in the study suggested that, based on the results of the review, two 5-day closures in October and November each year would provide sufficient protection for spawning reef fish and at the same time minimize socio-economic impacts, although the relevant biological data on stock condition prior to and during the closures, were not available for a robust decision. An important consideration, however, was to provide at least some protection to fish during their spawning period. The information from this report was provided to Fisheries Queensland who conducted a risk assessment to test the merits of the former and alternative spawning closure regimes. They considered the report and other information in formulating recommendations about spawning closures for the five year period 2009-2013. Taking into account stakeholder input, the Queensland Government introduced two annual 5-day closures around the new moons of October and November, as of 2009.

Summarized by Joy TL Lam
SCRFA
tllam.joy@gmail.com

For more information, please go to
[http://www.jcu.edu.au/ees/idc/groups/public/documents/newsletter/jcuprd_055976.pdf]

AUSTRALIA

The Grey Mackerel Fishery in Far North Queensland – an Update

Since 2006 this newsletter has recorded community observations relating to the on-going depletion of a grey mackerel (*Scomberomorus semifasciatus*) aggregation in inshore World Heritage waters of the Great Barrier Reef Marine Park, Australia. This is an endemic inshore species growing to around 1.2 m in length and favouring turbid waters.

Since 2003, local line trolling fishers have watched the size of seasonal, grey mackerel pre-spawning aggregations at Snapper Island, 2 km off the Daintree River estuary, shrink dramatically (see cover, bottom figure, part of a morning's catch, pre-2004). This followed the advent of offshore gillnetters using larger boats and targeting inshore grey mackerel aggregations around 2003.

Despite the Queensland Government's researchers previously advising that "mackerel stocks should be managed with **utmost caution**", netting of the aggregations continues.

There is no information about grey mackerel stock size, indicators of stock abundance and where the grey mackerel go outside the three months they aggregate on traditional inshore grounds, prior to spawning.

From November 2009 to March 2010, the local community attempted to develop an agreement between recreational, charter and commercial fishers on how much fishing should be undertaken by each sector. After two meetings this proposal was abandoned as being unworkable and unenforceable.

Members of the local community are calling for an immediate closure of the area for a period of two or three years to all fishing of grey mackerel, to allow for further research and for stocks to recover. It is proposed that if and when the stocks recover, the local fishery should be re-opened to line fishing only.

David C. Cook
Network for Sustainable Fishing, Wonga Beach, Australia
davecook@bigpond.com

*For the full story of the Network's campaign to save Queensland's stocks of Grey mackerel see:
[http://www.ffc.org.au/Grey_Mackerel.html#latest]*

PALAU

Spawning by Camouflage Grouper, *Epinephelus polyphkadion*, Observed and Documented in Palau for First Time in Wild

Observations of spawning in groupers are relatively rare, and the camouflage grouper is no exception. Its aggregations have been variously documented and monitored since the mid-1990's in Palau. However, observations of actual spawning had not been made there, despite many attempts to observe their spawning at dusk by different observers.

A recent dedicated effort by Jim Forrest and Jeanette Denby of the yacht "Dancer", based in Palau, offers for the first time solid information regarding the actual time of spawning by the camouflage grouper in the country. In addition to making general observations, Forrest was also able to film grouper behaviour, courtship and spawning for a new documentary being prepared by SCRFA on coastal fisheries and spawning aggregations in Palau.



Camouflage grouper © Yvonne Sadovy

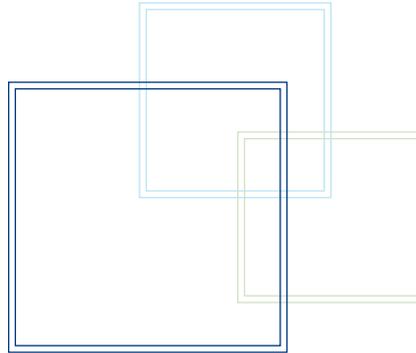
Spawning was seen on 11 June and 11 July 2010 (1 day before and the day of the new moon) at Ulong Channel (Ngerumkaol), a well known aggregation site on the western barrier reef of Palau, just after dawn. Spawning occurred after the tidal current had turned from incoming to outflowing. The currents were moderately strong moving out the channel and the grouper spawned over nearly an hour. Most spawnings were by a single pair, but a few group spawnings were also seen. There was not a general flurry of spawning; single pairs spawned at various times. In one case, a second male ("streaker") swam up to release sperm in the gamete cloud following a pair-spawn. The spawnings occurred a short distance inside the mouth of the channel (30-60 m distance) in water about 12 m deep. The groupers only ascended a short distance, 1.5-2 m, from the bottom.

In most cases black snapper, *Macolor niger*, were awaiting the spawn (they seemed to anticipate the spawn based on behaviour of the groupers) and moved into the newly released gamete cloud within seconds of release, feeding. Predation on a grouper within the aggregation was seen by Forrest when a large moray swam across the bottom, and took a grouper into a hole. Several sharks were attracted by this commotion, but did not attempt to seize the struggling fish.

The currents at Ulong Channel are somewhat unusual for a barrier reef channel, perhaps due to its "partial" nature; the channel does not go all the way through the shallow reef and is a net exporter of water, 60% is from lagoon to ocean, while 40% is from ocean to lagoon (import). We plan to reevaluate current observations around early morning times just before the new moon to determine the patterns of current flow when camouflage groupers are spawning.

Earlier work by Kevin Rhodes, based on fishing camouflage grouper at hourly intervals during the night and examining the gonads suggested that spawning also occurs during nighttime hours, so the time of the tide might be particularly important. Some excellent video footage of camouflage groupers courting and spawning was also included in the BBC Documentary series "South Pacific" in the second episode titled "Castaways". The documentary purports that the footage of spawning (time and date unreported) was shot in the Solomon Islands, however, an inquiry to the BBC revealed the footage was shot in French Polynesia and bought from a freelance videographer. Attempts to get more information about the location, timing, lunar phase and such have not yet been successful. We will keep tracking this down until we can add another positive observation on camouflage grouper spawning.

Patrick L. Colin
Coral Reef Research Foundation
crrf@palaunet.com



PERSPECTIVES

If there is one thing I have learned in over 20 years working with fish and fisheries, it is to be patient. Change, the kind needed for new approaches to management or acceptance of new ideas or ways of seeing the world, takes time.

SCRFA was formed a decade ago, and at the time I had high hopes that the, then, little understood phenomenon of spawning aggregations would shortly be, firmly and clearly, on the agendas of both marine conservation planners and fisheries managers. After all, spawning aggregations are key life history events and play a critical role in the reproductive capacity of many fish species, including several that are variously threatened. The majority of reef fish aggregations that are known are on the decline, and many colleagues would consider spawning aggregation management to be a “no-brainer” for a healthy fishery. Yet, despite considerable work this has not yet materialized, and aggregations are still not routinely managed or conserved globally.

However, there has been some progress. Encouraging examples are increasing of management action and even success with aggregation recovery, and there are many advances in our understanding of the biology of aggregating species. The reason, I believe, for such slow progress is that it takes a lot of time to assimilate and then ‘institutionalize’ new ideas. In the case of aggregations, a characteristic variously shared by many commercially important species, the gluts of fish taken while gathered to spawn have historically been the very basis of many fisheries. They also give, sometimes misleadingly, illusions of plenty in a fishery because of the large numbers of fish so obviously available over a short spawning period. Under such circumstances, it is often difficult to muster the public or political will to manage and limit extraction.

Accepting the need for managing despite apparent abundance witnessed when many fish are caught in an aggregation, is all part of the hard lesson we are learning that business cannot be ‘as usual’ in the future in our global marine fisheries. It takes time to acknowledge that we simply cannot continue taking as much as we want, when we want, and hope to still have plenty in the future. The lesson with aggregating species is proving to be a hard one to digest. We would certainly welcome ideas and comments on how to accelerate the process and get aggregations more widely on management, policy and conservation agendas globally.

Yvonne Sadovy
SCRFA
yjsadovy@hku.hk

NEW PUBLICATIONS

Albins M.A., M.A. Hixon, Y. Sadovy. (2009). Threatened fishes of the world: *Epinephelus striatus* (Bloch, 1792) (Serranidae). *Environmental Biology of Fishes* 86(2) DOI: 10.1007/s10641-009-9512-5

Baumberger R.E., N.J. Brown-Peterson, J.K. Reed, R.G. Gilmore (2010) Spawning aggregation of beardfish, *Polymixia lowei*, in a deep-water sinkhole off the Florida Keys. *Copeia* 2010, 1: 41–46

Colin P.L. (2010) Aggregation and spawning of the humphead wrasse *Cheilinus undulatus* (Pisces: Labridae): general aspects of spawning behaviour. *Journal of Fish Biology*, 76: 987–1007

Erisman B.E., M.T. Craig, P.A. Hastings (2010) Reproductive biology of the Panama graysby *Cephalopholis panamensis* (Teleostei: Epinephelidae). *Journal of Fish Biology*, 76: 1312–1328

Hutchinson N. & K.L. Rhodes (2010) Home range estimates for squaretail coral grouper, *Plectropomus areolatus* (Ruppell 1830) *Coral Reefs*, 29(2): 511-519

Karras C. & J.J. Agar (2009) Cruzan fishers' perspectives on the performance of the Buck Island Reef National Monument and the red hind seasonal closure. *Ocean & Coastal Management*, 52: 578–585

Kobara S. & W.D. Heyman (2010) Sea bottom geomorphology of multi-species spawning aggregation sites in Belize. *Marine Ecology Progress Series*, 405: 243–254

Luckhurst B.E. (2010) Observations of a black grouper (*Mycteroperca bonaci*) spawning aggregation in Bermuda. *Gulf and Caribbean Research*, 22: 43-49

Nanami A., K. Okuzawa, H. Yamada, N. Suzuki, Y. Aonuma (2010) Reproductive activity in the checkered snapper, *Lutjanus decussatus*, off Ishigaki Island, Okinawa. *Ichthyological Research*, DOI 10.1007/s10228-010-0155-5

Phelan M. (2010) Interim 2010 goliath grouper monitoring results Jupiter, Florida. [Download link: http://www.scrfa.org/images/stories/scrfa/EdOut/news/interim_2010_goliath_grouper_monitoring_results.pdf]

Sadovy de Mitcheson Y., M. Liu, S.Suharti (2010) Gonadal development in a giant threatened reef fish, the humphead wrasse *Cheilinus undulatus*, and its relationship to international trade. *Journal of Fish Biology*, 77: 706–718

Sanches E.G., C.V. Pannuti, E. F. Sebastiani, J.A. Rodrigues-Filho, C. Eduardo de Oliveira Garcia, R.G. Moreira (2010) Threatened fishes of the world: *Mycteroperca microlepis* (Goode & Bean, 1880) (Serranidae: Epinephelinae). *Environmental Biology of Fishes*, 87:317–318

Semmens J.M., C.D. Buxton, E. Forbes, M. J. Phelan (2010) Spatial and temporal use of spawning aggregation sites by the tropical sciaenid *Protonibea diacanthus*. *Marine Ecology Progress Series*, 403: 193-203

Takemura A., M.S. Rahman, Y.J. Park (2010) External and internal controls of lunar-related reproductive rhythms in fishes. *Journal of Fish Biology*, 76: 7–26