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CONNECTIVITY IS EVERYTHING

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ABSTRACT: Here I review some of the changes that have occurred in coral reef fisheries, both in the priority focus areas and in the methods and resources available, as viewed through the personal perspective of my 37 years working in Puerto Rico. The development of marine protected areas (MPAs), especially no-take areas, as management tools and the expansion of fisheries management beyond populations to embrace ecosystem-based management (EBM) are both driven by (1) the expansion of stressors, including fishing, beyond the effective capacity of most agencies and (2) the close linkages between fisheries resources and their supporting habitat. Underlying both is the maintenance of the productive capacity of the coral reef ecosystem. Understanding what makes an ecosystem productive requires knowledge on all the pieces, how they are connected and the processes determining the direction and rates of flow (of nutrients, individuals, biomass, ecological function) through the seascape. Principles of connectivity are thus critical for the design of MPAs, MPA networks, and maintaining productivity through EBM.

KEY WORDS: Ontogenetic migration, MPA design, ecosystem-based management, habitat connectivity, coral reef fishes

I am a generalist. A generalist tends to know nothing about everything. For a generalist, there is nothing like looking retrospectively back on your career to illustrate how little you think you've accomplished relative to what you wanted to do if you had just kept focused on the topic at hand. However, being a generalist allows one to be synthetic, and connectivity is a synthetic concept.

INTRODUCTION

Connectivity is all about flow: the rate and direction of that flow, and the distance over which it occurs. In the marine environment flow can be through the movements of currents transporting dissolved and particulate matter or passively drifting organisms, or through the active movement of swimming or crawling macrofauna (e.g., Francis and Côté 2018). Connectivity occurs across a broad expanse of spatial and temporal scales, connecting regions and local habitats. While we normally think of connectivity in terms of the transport of nutrients and organic matter, either spatially or through trophic networks, ecological functions such as predation and herbivory can also be transported. Connectivity begets productivity. Examples from the human economy abound. Towns located along railroad lines developed into cities, those as airport hubs became megacities, especially coastal cities that could also support the ever-larger vessels used in maritime trade. Within cities, neighborhoods with subway stations developed greater and more diverse economies (see West 2017 on how cities grow).

My purpose here is to explore the evolution of fisheries biology in coral reef ecosystems, albeit through the narrow and biased lens of my personal experience. This evolution is overlain on the substantial changes over the past 40 years brought about by the advent of computers, the internet and technological advances that have revolutionized how we do science, but my focus will be on what science we do, and how I come to claim that connectivity is everything.

IN THE BEGINNING

I received my graduate training at the University of Rhode Island's Graduate School of Oceanography (GSO) under the tutelage of Saul Saila. My research interests were in marine populations, and this training took place within an environment decidedly focused on quantitative stock assessment and the basic population parameters that underlie this, including the effects of environmental variability. The quantitative nature of much of this work pushed the limits of computing power that existed at that time. The GSO was, and remains, a state of the art facility, and during my time there its computing resources transitioned from punch cards, to teleprinter terminals to interactive CRT screens; I was among the first to type my dissertation on a computer. For my dissertation work I was able to do length-frequency analysis using a Dupont 310 Curve Resolver, a nifty analog computer, for which I wish there was a digital version available.

While my graduate training gave me a varied and quantitative background, I feel I strayed from the direction most others were going. Some of this was because I was working with mollusks, not fish (I did undergraduate work at Rutgers University's New Jersey Oyster Research Lab at both the Bivalve and Cape Shore facilities), but also because I developed an interest in life-history strategies. I wanted to go beyond the quantitative assessments of growth and mortality parameters to understand their biological relationships and how these were driven by life histories, including the impacts of exploitation.

REEF FISHERIES BIOLOGY IN PUERTO RICO

My first, and as it turned out only, permanent position came in 1981 when I was hired as an assistant professor in the Department of Marine Sciences, University of Puerto Rico at Mayagüez. In some sense I followed a well-established connection between GSO and Puerto Rico, having been preceded by John Martin (Martin 1970), Jim Parrish (Parrish 1982) and Dave Stevenson (Stevenson 1978). I felt reasonably prepared for this transition, as URI, including Saul Saila, had a particular focus on tropical fisheries (e.g., Saila and Roedel 1980). However, much of that was, well, academic.

Puerto Rico was my first real introduction to tropical reef fisheries, and what I found was fairly typical of the region. At that time, fishing pressure was very high (and landings were about to collapse; Appeldoorn and Sanders, 2015). My anecdote illustrating this was that it was impossible to travel to any site on the outer platform in a straight line because the density of fish trap buoys made the run more of a giant slalom event. To its credit, Puerto Rico had a well-funded Fisheries Research Laboratory that both compiled landings statistics and conducted field surveys and research. Unfortunately, the former grossly underestimated actual landings (SEDAR 2009), while the latter showed a mixed record of often good work (e.g., Abgrall 1975, Erdman 1976, Boardman and Weiler 1979) conducted in the absence of a management context. Puerto Rico had no modeling or stock assessment capacity, and policy was implemented in the central government, generally without the input from fisheries professionals (Kimmel and Appeldoorn 1992). What policy existed focused exclusively on development; Puerto Rico's fisheries law dated to 1936.

While this situation was typical, fisheries biology in reef ecosystems was advancing rapidly. John Munro's classic and extensive work in Jamaica (later summarized in Munro 1983) demonstrated the power of directed research in support of management questions and validated the application of standard fisheries techniques and models (e.g., yield-per-recruit, surplus production) to tropical fisheries. Daniel Pauly spearheaded the application of length-frequency analysis for estimating growth, mortality, recruitment patterns and selection, developed empirical relationships among von Bertalanffy growth coefficients, and among these and natural mortality, thus providing needed inputs for basic YPR calculations (Pauly and David 1981, Pauly 1984, Pauly and Morgan 1987).

Having a strong background in length-frequency analysis and quantitative methods, I was eager to apply these approaches in Puerto Rico, naively thinking this would foster science-based fisheries management. However, there were a number of logistical constraints. When I arrived in Puerto Rico I was set up at the department's Magueyes Island Marine Laboratory, located off the south coast town of La Parguera on its own island, which was (and still is) only accessible by a short boat ride. The location and accompanying facilities were ideal for conducting field-based laboratory classes and research,

but there were down sides early on. My initial space consisted of a single 10x8-ft room located immediately adjacent to the central air conditioner, so everything vibrated. There was only one telephone for the whole island, located in the secretary's office (talk about lack of connectivity!). After 3:30 pm, the phone was placed in a locked box in the door, so if you had to make a call after that you had to make arrangements to get the key ahead of time; there was no place to sit or to write on the sidewalk, and the box was low enough that the phone cord did not stretch to my standing position. The lone photocopier was in the departmental office in Mayagüez, an hour's drive through the sugarcane fields. The department did have a specialized marine sciences library, also in Mayagüez, but access to literature was still difficult, and I always planned at least one full day of library work when traveling near a major marine institution. The internet was still more than a decade away. When I arrived, the island had only one Apple II computer, with 64k of memory, and that was bought by a consortium of students. Fortunately, our director at the time, Manuel Hernandez-Avila, was an effective lobbyist both within the university and out (we were the only wholly graduate department and only doctoral program in Mayagüez), and with a core of young and talented faculty the department was a dynamic environment. New space was constructed; grants supported the influx of desktop computers. Magueyes Island eventually became a facility where fully modern scientific laboratories were located with immediate access to the tropical marine environment. This was truly a unique place.

The early 1980's was also a time of extreme interest in the mariculture of queen conch, *Lobatus* (= *Strombus*) *gigas*, an iconic Caribbean species that was overfished in many locations. I was fortunate to land in a situation where my colleagues Paul Chanley and David Ballantine were successfully rearing larvae, but they had little idea what to do with the resulting juveniles. Thus began my long-term love affair with queen conch, developing a line of research to provide data useful for management. We started out doing mark-recapture release experiments with the hatchery-reared juveniles to study growth, mortality, movements, and the effects of size on these processes (Appeldoorn 1984, 1985). This led to similar studies on the wild population, employing both length-frequency and mark-recapture techniques (Figure 1), with the added twist that conch change their form of growth at the onset of maturity from an increase in length to an increase in the thickness of the shell lip (Appeldoorn 1987, 1988a,b, 1990, 1992a). While the two-phase growth structure of conch was challenging, it was matched by the strong environmental influence on conch growth, and hence, on size at maturity, rendering much of my quantitative work heuristically useful, but not necessarily directly applicable for local stock assessment. Also interesting was that natural mortality seemed to decline gradually with age (Appeldoorn 1988b) – an assumption violation of most fisheries models at the time!

FIGURE 1. Author measuring shell lip-thickness of a tagged queen conch. Note home-made caliper on the bottom, used for measuring shell length (photo credit: D.L. Ballantine).

We also did some interesting experiments on the role of sexual facilitation on egg production, in which we enclosed conch on a natural spawning ground in treatments varying in sex ratio and density, and then calculated the number of eggs spawned by each and every female for the full spawning season. My doctoral student, Shawna Reed, was the one out there every day collecting egg masses. While the sexual facilitation part did not work out so well due to a number of males being not yet mature, we were able to establish baseline information on fecundity, egg mass deposition rates and the relationship between lip-thickness and maturity. These showed conch to be much more fecund than previously estimated (our "super spawner" produced the most egg masses (25), the most eggs (22 million), the largest single egg mass (1.48 million), and had the longest reproductive season, spawning both the first and the last egg masses during the season), but also that reproductive output could be significantly less if density was high enough to limit food supply. These results were cryptically published in Posada et al. (1997). This raises another hard-learned lesson about connectivity: if you want your work to be circulated, known, and used, you have to publish, something I continue to struggle with.

One major point of all this was that it was fun. La Parguera was a great place to do research. I was active in the field and attracting a hoard of graduate students willing to work on a wide variety of projects. My first student to finish, Zelma Torres, conducted Puerto Rico's first field survey of conch density and abundance, focusing on the southwest platform. Three other early graduate students, Ken Lindeman (technically not mine), George Dennis and Jay Rooker, did fundamental work on juvenile and adult grunts (*Haemulidae*), a group that became another focus in my lab as a model for reef fish. I got my first modeling grant to develop a multispecies model, based on grunts (Appeldoorn 1996), and used it to trade in my Apple II+ with 128k of bank-switched memory and twin 5¼" floppy

disk drives for an IBM XT with 256k of memory and a 10Mb hard drive.

Working with students is certainly one of the most rewarding, but challenging, and at times scary aspects of my position. It was challenging in the sense that I often had upward of 10 students at a time that needed to be advised, directed, and trained. Fortunately, over the years it became apparent that after some critical mass of students was achieved, the new arrivals relied heavily on the senior students for much of this. I was also able to rely on colleagues to help oversee aspects of research for which I had no particular expertise. What was scary? A number of my students were clearly smarter than me, and others much more energetic, and I felt pressure to keep up with them, least that they think their advisor was an idiot – not sure I always succeeded.

One interesting and fun side project arose when helping my colleague, Dannie Hensley, do deep water trapping, up to 1,000 m. Being an ichthyologist, he was interested in fish, but what he caught a lot of was crustaceans, including a number of pandalid shrimps and the giant isopod, *Bathynomous giganteus*. I built some traps designed to catch shrimp, which they did, but in a fair turnaround, what they also caught efficiently were hagfish, including a new species (Hensley 1985). I remember seeing the shrimp traps coming up from depth in clear tropical water dragging a 2-m long trail of copious hagfish slime. This was all low-tech work; we just dropped the trap set over the side with a kilometer of polypropylene line and surface buoys. Hauling back was via a pot-hauler on our very round-bottomed Thompson trawler, with the line being hand coiled and thrown periodically in a series of galvanized wash tubs. On one occasion when the hydraulic line sprung a leak I deftly coiled the line as I slid frictionless from one side of the rolling

vessel to the other; everyone else grabbed on to something for control, attempting to avoid slipping or being hit by sliding traps, tubs of line or sample buckets. The neat thing, however, was that this project led to a Sea Grant facilitated collaboration with NOAA that brought the Submersible Johnson Sea-Link (Figure 2) to Puerto Rico and the US Virgin Islands (Nelson and Appeldoorn 1985). I got to dive down to 800 m to see shrimps, isopods and sharks in action, and how cool is that!

FIGURE 2. The author emerging from the submersible Johnson Sea-Link in 1985 (photo credit: D.L. Ballantine).

IS THIS WORKING?

Despite the above work and still other studies focused on stock status (e.g., Acosta and Appeldoorn 1992, 1995, Appeldoorn 1992b), the fun was tempered by the little traction evident in improving actual fish stocks or influencing fisheries management. By the early 1990's catch rates in Puerto Rico had already declined markedly across the board, and it was clear that scientifically documenting overfishing was not going to lead to any sufficiently rapid change. There were structural problems in the management of fisheries in Puerto Rico (Kimmel and Appeldoorn 1992). Changing these would require sustained efforts elsewhere, with no guarantee of success, and my interests and responsibilities (i.e., training graduate students) were not aligned to that task. In addition, landings data continued to be plagued by poor quantity and quality of information to a degree that limited any advanced modeling efforts. Meanwhile, quantitative stock assessment was developing new procedures (e.g., Fournier and Doonan 1987), partly fueled by the increasing power of desktop computers. Due to the lack of applicability, the increased emphasis on computer modelling, and my already established emphasis on field work, I became more detached from this community. Re-enforcing this trend, of course, was the clear advantages of working in La Parguera, with its immediate access to a variety of marine environments from rocky shores and mangroves to depths over 1000 m. This also attracted field-oriented students that were not necessarily interested higher end stock assessment. At the same time, severe ecosystem disruptions were becoming evident due not only to overfishing, but also to disease impacts and collapse of the coral *Acorpora palmata* and the urchin *Diadema antillinum*, as well as enhanced terrestrial runoff that were resulting in a significant alteration in reef communities, and potentially the productive capacity of the system. Was there another way forward?

That question got answered through the efforts of Jim Bohsack, Bill Ballantine, Callum Roberts and others who were developing the theory and application of using no-take marine reserves in fisheries management (Plan Development Team 1990, Roberts and Polunin 1991, Ballantine 1991). The appeal of marine reserves was as simple as it was comprehensive. Key among these was that it simplified enforcement to a single fishing or not-fishing assessment, while addressing important management goals such as reducing fishing effort, conserving spawning biomass, and providing control areas to assess fishing impacts on both the population and community. There were also substantial non-fishery related benefits (Bohsack 1998), including helping to refocus management to address environmental degradation. To me, two aspects stood out. The first was the possibility of preserving at least some portion of a stock before total collapse occurred; that is, save some places while we figure out how to get effective management regimes in place. This was basically triage applied to where I saw the future heading. The second was the role of reserves as control areas; if we could not conduct quantitative assessments to determine theoretical refer-

ence points, we could at least monitor population parameters such as size structure and density (something biologists were actually good at) between fished and unfished areas and use the difference to quantify stock status.

ALL IN ON MARINE RESERVES

By the mid-1990's I had refocused the research efforts of my lab, my graduate teaching, and my scientific advocacy work toward marine reserves, trying to develop design criteria and examining assumptions on marine reserve function. The latter was not easy given we had no closed areas in Puerto Rico to conduct such research. Nevertheless, these were heady days, as the theory and practice were all new, and my research could contribute to a potential management strategy that aligned with what I saw on the reef and with what I thought might be locally possible from a policy perspective. The theory and practice (and malpractice!) of marine reserves created a whole new front for research, one often led by fish ecologists rather than by fisheries biologists (e.g., Crowder et al. 2000, Sale et al. 2005). And while I was eager to be a part of that effort, I am always constantly reminded that management success is achieved through the combined actions of people working at various levels, from those doing high-end, perhaps theoretical science to those on the ground working in the particular areas and with the particular communities where change is being sought. I felt I was somewhere in between, trying to move science but also trying to move actual management, both locally and regionally. For the latter, I convinced the University of Puerto Rico Sea Grant College Program to develop a Marine Fisheries Reserve initiative, pushed symposia at the Gulf and Caribbean Fisheries Institute (e.g., Appeldoorn 1998, Appeldoorn et al. 2003), and supported creating protected areas in Puerto Rico.

Much of my early research here was centered around temporal patterns of fish-habitat associations. If we wanted to protect overfished species using space-based management, we needed to know what species occurred where and for how long. While this is something reef fish ecologists had studied, it was new for fisheries management. At the time, Conrad Recksieck and I were studying the movement of juvenile White Grunt (*Haemulon plumieri*) in and out of resting schools that occurred on back and fore-reef areas. In studying these resting schools, we noticed their location, as well as fish behavior, varied by fish size. Expanding on this, and bringing in earlier feeding studies, we were able to put together a pattern of differential habitat use over ontogeny, and then put this ontogenetic migration into a context for marine reserve design (Appeldoorn et al. 1997). We were not the first to notice this, as early work in St. Croix by Ogden and Ehrlich (1977), Brothers and McFarland (1981) and Helfman et al. (1982) had effectively, but not formally, described similar ontogenetic stages for the French Grunt (*H. flavolineatum*). Nor were we the only ones researching changing habitat-fish associations during ontogeny. A major and prolific effort focused in Curaçao similarly started by examining chang-

es in size structure of a variety of fishes among habitats across a mangrove–seagrass estuary to reef gradient (e.g., Nagelkerken et al. 2000a, Cocheret de la Morinière et al. 2002). Dahlgren and Eggleston (2000) not only illustrated the habitat shifts of Nassau Grouper (*Epinephelus striatus*), they also showed that the timing of those shifts followed the theoretical predictions of Werner and Gilliam (1984) based on trade-offs between shelter from predation versus access to food supply for growth.

From here we launched an ambitious program to describe differential habitat use of reef fishes through ontogeny, focusing on snappers, grunts, groupers and parrotfishes. But, one of the major stumbling blocks we encountered was that there were no detailed habitat maps for La Parguera, although aerial photographs were helpful. Our initial “break-through” came when Ken Lindeman introduced us to his concept of the Cross-Shelf Habitat (CSH) matrix (Lindeman et al. 1998), which plotted habitat type (e.g., mangrove, sea grass) on the vertical axis and location across the shelf on the horizontal axis. Once we had a framework for organizing our field work, we threw my whole lab into the task of conducting visual transects across the shelf and mapping both the location and amount of habitat within the transect and where each fish occurred relative to that habitat, trying to hit as many boxes on the CSH matrix as we could, with replication. This went on for several years, with gracious support from University of Puerto Rico Sea Grant and NOAA/NCCOS, with one lucky student putting it all together for her Master’s thesis (Cerveny 2006), showing in matrix space how species changed their habitat

use (type and location) during ontogeny (e.g., Figure 3).

TECHNOLOGY COMES TO THE FIELD

Our initial work was laid out in matrix space, which was scientifically illuminating, but lacked key information helpful for determining how fish move through their immediate environment. This requires actual habitat maps that quantify the amount and exact location of different habitats and their position relative to other habitat types. This became possible around the turn of the

FIGURE 3. Distribution and relative abundance in La Parguera Puerto Rico of Ocean Surge wrasse (*Acanthurus bahianus*) for 3 life stages by habitat type and cross-shelf strata. Line at top indicates the depth profile. “X” indicates stratum not sampled. Pink boxes indicate habitat-strata combinations that do not occur. Relative abundance is by quartile, with darker blue colors indicating higher abundance. For cross-shelf strata: Thick vertical lines separate the three shelf zones divided by emergent reef lines. Thick horizontal lines separate habitat types into higher categories of submerged aquatic vegetation, unconsolidated sediment and consolidated sediment. Modified from Cerveny (2006).

century with the advent of the Global Position System (GPS), synoptic sensors such as aerial, satellite, or sonar imagery, and appropriate software, particularly Geographic Information Systems (GIS). In the spring of 2001 I took a half sabbatical to learn GIS and also familiarize myself more with landscape ecology, which was providing exciting ways to look at connectedness in relation to habitat structure.

There were two efforts to develop habitat maps off La Parguera, which were conducted simultaneously. One was led by NOAA/NCCOS and was based on aerial photography. This was a massive collaboration and resulted in habitat maps at 4,000 m resolution for Puerto Rico and the U.S. Virgin Islands (Kendall et al. 2001), as well as follow-up surveys to document fish and benthic communities associated with the major habitat types (Christensen et al. 2003, Pittman et al. 2010). The second mapping effort was a collaboration with Jose Rivera and my doctoral student, Martha Prada, using small-boat-based sidescan sonar technology (Prada et al. 2008). This was a much finer scale effort both in resolution (4 m) and spatial scale (a 3 nautical mile wide swath from the shoreline to the shelf edge), but it had the advantage of filling in the holes in deep or turbid areas where bottom features were undetectable in aerial photographs.

QUANTIFYING SEASCAPE EFFECTS

With detailed habitat maps, it was now possible to go beyond fish-habitat associations and start to see how fish distributions were affected by the surrounding seascape. By examining fish movements in relation to habitat distributions one could now identify factors defining potential migration corridors and quantifying the rates of movements across habitats. For example, Kendall et al. (2003) were able to show that the presence of the French Grunt on patch reefs was related to the amount of surrounding feeding habitat within 100 m and that the probability of occurrence fell to near zero if feeding habitat was further than 300 m, suggesting that this was the limit of their characteristic twilight feeding migrations (McFarland et al. 1979). We did similar work in Providencia, Columbia, showing that the biomass of grunts and snappers on patch reefs were positively related to the amount of feeding habitat within 500 m (Appeldoorn et al. 2003). We additionally showed that community structure was also related to distance from presumed near-shore nursery areas (e.g., mangroves, seagrass, rocky shorelines), indicating that some species were limited to the degree or direction they would migrate out from where they settled. My doctoral student, Schärer-Umpierre (2009), found similar limitations in fish distributions around Mona Island, Puerto Rico. Pittman et al. (2007) demonstrated how the mangrove fish communities in La Parguera were affected by the composition of the surrounding seascape, and that the spatial scale and location of this effect varied among species. For example, juvenile Yellowtail Snapper (*Ocyurus chrysurus*) densities were highest on offshore mangroves where there was abundant seagrass and coral reef within 100 m. In contrast, juvenile Gray Snap-

FIGURE 4. Mean cross-habitat boundary transfer rates of fish prey (g/100 m gillnet length) off La Parguera, Puerto Rico. Arrow widths scaled to transfer rate. Reef-Unconsolidated boundaries were not sampled. (Unpublished data from Roque, Clark and Appeldoorn). See Clark et al. (2009) for study details.

per (*Lutjanus griseus*) preferred extensive onshore mangroves, also with a high proportion of seagrass, but now out to a range of 600 m. Probably the most ambitious study was to quantify, at least preliminarily, the nocturnal movement of subadult and adult fishes and their transport of prey across habitat boundaries. Clark et al. (2009) set 100 m gillnets ($n > 200$) along habitat boundaries (seagrass, reef, mangrove, unconsolidated sediment) before sunset and retrieved them after sunrise. The orientation of the fish in the net gave their direction of travel, while weights of these fish and their identified gut contents gave the biomass of fishes and prey moving across these habitat boundaries (Figure 4). Thus, we could identify which species and trophic groups were the major vectors of transport.

Meanwhile, work in Curaçao had similarly expanded to test the impacts of seascape connectedness, specifically from near-by seagrass and mangrove nursery habitats to reef fish communities (e.g., Nagelkerken et al. 2002, Dorenbosch et al. 2004), eventually quantifying limits to alongshore ontogenetic migration away from nursery areas (Dorenbosch et al. 2007) and limits to daily migrations to feeding habitats (Nagelkerken et al. 2008). Additionally, they started looking at the functional roles of different habitats, comparing, for example, the shelter versus feeding roles of seagrass beds and mangroves (Nagelkerken et al. 2000b, Nagelkerken and van der Velde 2004a,b). Similarly, Mumby et al. (2004) documented mangrove nursery habitat dependence for a number of species, then developed a series of algorithms describing where and to what degree man-

grove nurseries enhance reef fish communities (Mumby 2006).

WHERE DO THOSE FISH GO, ANYWAY?

At this point, most of our knowledge of reef fish connectivity through ontogenetic migration was inferred from differences in abundances and size structures in different habitats or locations across the platform. These inferences were certainly stronger where lack of abundance could be related to lack of presumed nursery habitat. Nevertheless, as pointed out by Beck et al. (2001) identification of critical habitats, such as nursery areas, should account for (1) differences in the areal extent of habitats (e.g., a mangrove fringe versus a vast expanse of seagrass), and (2) differences in survival, i.e., the area with the highest abundance may not contribute the most to the next stage/location. Mateo et al. (2010), working off La Parguera and St. Croix, attempted to address these questions by using otolith microchemistry to classify the nursery habitat of forereef subadults. They showed that up to about 70% of French Grunts and almost 100% of Schoolmasters (*Lutjanus apodus*) at both sites originated from mangrove (as opposed to seagrass) nursery areas, even though in both areas seagrass occurred in much greater abundance.

A third problem relying on inferences from differential size distributions was that actual migration pathways were unknown, except where geomorphology imposed strict limitations, e.g., Curaçao. How did fish move from inshore areas to offshore? Did they take the shortest route, follow acoustic cues, move up-current following olfactory cues, follow habitat corridors, or some combination of all? Juvenile grunts had been shown to use compass direction (Ogden and Quinn 1989) and visual cues

(Helfman and Schultz 1984) in twilight migrations and, later, to be able to differentiate nearshore versus offshore water (Huijbers et al. 2008). Orientation and movement capabilities were important from the perspective of marine reserve design: where did the fish in a reserve come from, and where did they go if they left the reserve?

This is where I next focused my attention, using conventional and acoustic tagging and tracking techniques. I was interested in determining if there were general rules governing fish movements. Early work tracking White Grunt off La Parguera and Key Largo, Florida (Tulevech and Recksiek 1994) suggested that movements were strongly affected by habitat discontinuities, habitat arrangement and habitat boundary contrasts. Bouwmeester (2005), using coded-wire tags, was able to serially track small juvenile French Grunt (6–13 cm) as they migrated out from backreef nursery areas through a series of resting schools toward the inner forereef. The primary direction of movement was up-current, but along the reef margin to the east (see Appeldoorn et al. 2009). This was significant as this potentially would lead to a later offshore migration using a different set of reefs than if they had followed the opposing reef margin to the west (Figure 5).

Another student, Stephanie Williams, conducted a series of experiments tracking subadult and adult White Grunt on several spatial scales. One of the goals was to determine how they react to habitat boundaries (Wiens 1992). In a series of displacement experiments, she found that the ability to return to point of origin was facilitated by short displacement distance, larger body size, the availability of intermediate patch reefs, and learning (Williams 2011). Visual observations subsequently indicated

FIGURE 5. Mean ontogenetic migration of juvenile French Grunt (*Haemulon flavolineatum*). Inset on left: Migration from Majimo, an inshore reef in La Parguera, Puerto Rico. Black dots indicate locations of daytime resting schools. Black arrows are the initial tracks of off-reef twilight feeding migrations. White line indicates the primary migratory path as determined by mark recapture studies ($N = 31$ recaptures; initial size range: 7.9–13.7 cm FL; days at liberty: 34–239). Area shown is indicated in the white box to the right. Right: Two potential pathways for ontogenetic migration from Majimo leading to 2 different reef complexes.

that these intermediate patch reefs facilitated cross-boundary movements by acting as stepping stones to enhance connectivity. Similar results on a smaller scale were found for the Longfin Damselfish (*Stegastes diencaeus*) by Turgeon et al. (2010). Subsequent large-scale tagging studies have supported these findings. For example, Kendall et al. (2017) found fishes in Coral Bay, USVI to generally avoid crossing a broad sand channel in favor of moving along the sides; those fish that did cross seemed to do so where intermittent patch reefs occurred within the channel. Pittman et al. (2014) used the concept of habitat corridors to model potential travel distances between home ranges and a spawning aggregation site.

Looking at diurnal movements over longer periods of time, Williams found that White Grunt periodically shifted their spatial use patterns within a larger area, using one area intensively over a period of several days or weeks before shifting to another area (Williams 2011, Appeldoorn et al. 2009). Nevertheless, movements seemed to be limited to a home range within ~300 m from the backreef to forereef zones along reef margins. A similar behavior of shifting patterns of diurnal habitat use was observed for Bluestriped Grunt (*H. sciurus*; Beets et al. 2003, Friedlander and Monaco 2007). These studies clearly showed that short term observations would significantly underestimate an individual fish's home range, and that fishes had a large degree of flexibility in their spatial use of habitat. But they also suggest that fish may exhaust their prey supply locally, thus requiring movement to other areas, with movement back to the original area further suggesting that prey levels can recover. These movement observations, then, provide the underlying explanations for the previously observed relationships between fish occurrence or density and the amount of available surrounding feeding habitat.

Rooker et al. (2018) tracked the movement of Schoolmaster and White Grunt in relation to both habitat and the distribution of a predator, the Great Barracuda (*Sphyrna barracuda*), within a back-reef nursery. The grunt and snapper restricted their movements to areas not occupied by Great Barracuda, who patrolled the open channel during the day. As such, the prey species were found along mangroves and on patch reefs during the day, and only ventured across a sand channel and into feeding grounds within the seagrass at night, when the Great Barracuda left the area. Thus, while species diversity may be higher where high habitat diversity exists (Pittman et al. 2007), actual movements among habitats are tightly controlled by the distributions of both those habitats and the risk of predation.

Large-scale studies over long time periods (Pittman et al. 2014, Kendall et al. 2017) have shown that fish species are quite variable in their movements. In the former study, 17% of the fish tagged moved distances of > 1 km in a single day, with 3 individuals traveling over 10 km in a single day (Saucereye Porgy (*Calamus calamus*), Lane Snapper (*L. synagris*), Bluestriped Grunt). Over much longer time frames distances traveled in-

creased, with 75% moving more than 1 km and 33% moving more than 5 km. In comparing movements to the dimensions of Eastern Caribbean marine protected areas (MPAs), Pittman et al. (2014) found that 74% of fishes (16 species) moved greater distances than dimensions of 40–64% of MPAs, and 28% (12 species) traveled distances greater than the dimensions of 69–85% of the MPAs. They emphasize a potential scale mismatch, although actual applications of their results will depend on the specific geomorphology of each MPA, which scales the degree of movement, and the trade-off between the goals of protection versus spillover. Nevertheless, the implications of incorporating the movement of fishes into MPA design are clear. Di Franco et al. (2018) showed that significant increased densities within Mediterranean marine reserves occurred only for those cases where reserve size was larger than species home range.

One of the more extreme examples of movements and connectivity is the formation of large transient spawning aggregations, where upwards of 10,000's of fish may converge to a single location. Distances traveled to/from such aggregations can be substantial, i.e., up to 33 km for Red Hind (*Epinephelus guttatus*, Nemeth et al. 2007), 40 km for Mutton Snapper (*Lutjanus analis*, Pittman et al. 2014), and 220 km for Nassau Grouper (Bolden 2000). Nemeth (2012) and Erisman et al. (2015) reviewed the ecological implications of these events. For larger fishes such as snappers and groupers, there is a progressive, large-scale movement of fish from resident habitats over a broad catchment area (up to 100 to 1,000 km² to a narrower staging area (10 to 100 km²), to eventually a courtship arena (< 10 km²) and finally a site (1 km²) where actual spawning occurs. Final densities can exceed 8,000 kg 100 m⁻². These sites not only serve as point-sources for larval dispersal, they also function as point sources for intense feeding activities by both the aggregating individuals and by predators on both the spawners and the eggs. Of the latter, Whale Sharks (*Rhincodon typus*) are frequent visitors at spawning times to multispecies aggregations sites (Heyman et al. 2001). Of the former, predatory sharks are frequent visitors (Pickard et al. 2016), as is, of course, man (Sadovy de Mitcheson 2016). Spawning aggregations thus are an important conservation concern, and their inclusion into marine reserves has been advocated frequently (Grüss and Robinson 2014).

LARVAL CONNECTIVITY – GOING WITH THE FLOW

While I do not intend to review the scientific progress and knowledge of fish larval dispersal nor enter the debate as to whether reef fish populations are open or closed, the magnitude and dispersal distance of larval recruitment is important when considering marine reserve design, as reserves should be planned in a network context. Only recently has specific information on larval dispersal capabilities become available. Field studies have shown the potential for self-recruitment on island scales (Jones et al. 1999), even for species with long larval duration periods (Swearer et al. 1999). Detailed hydrodynamic models have consistently lowered the expected distance of dis-

TABLE 1. General characteristics of ontogenetic migrations in coral reef fishes and their management and conservation implications.

Characteristics of Ontogenetic Migrations	Management and Conservation Significance
Many coral reef fishes use different habitats during ontogeny, including most larger, commercially important species	Ontogenetic migration is important for fisheries management. Essential Fish Habitat (EFH) designations must consider all life stages.
Some species show a degree of habitat-specific dependence, but most show a varying degree of habitat plasticity	For most species, spatial management can be flexible, but some habitats are required if present: mangroves, sea grass
Ontogenetic migrations are generally characterized by inshore to offshore movement	Spatial conservation and management need to include the extent from shoreline to shelf edge
Ontogenetic dispersal alongshore is more limited than dispersal offshore	There are spatial limits to connectivity
Degree of daily and ontogenetic migration varies by species	Management and conservation need to be scaled to those species with the greatest range of movement
Habitat boundaries and corridors effect the direction and distance moved	Habitat continuity/isolation is an important design criterion for spatial management
Species distributions are a function of local habitat and seascape factors	EFH needs to be examined and defined on different spatial scales
Individual species movement and distribution patterns can be similar despite large differences in seascape characteristics	General species-specific rules for distribution and movement are possible
Areas with higher habitat diversity support a greater abundance and	Management should focus on areas of high habitat diversity

persal as they have incorporated more specific information on larval behavior and mortality, showing expected distances to be between 10 and 100 km (Cowen et al. 2006), the level used by Sala et al. (2002) as a limit for connectivity among protected areas. For Puerto Rico, effective dispersal distances were even less (Pagán López 2002), and we used a limit of 35 km when applying results to reserve network design. With the advent of next-generation DNA sequencing techniques, measured effective dispersal distances have declined even further. Planes et al. (2006) measured genetic dispersal out to 35 km, sufficient to maintain connectivity within a network of MPAs. In Puerto Rico, Beltran et al. (2017) measured an effective dispersal distance of only 10 km per generation for the Yellowhead Jawfish (*Opistognathus aurifrons*). This is consistent with the lower end observed in other species, but much less than observed, for example, in the French Grunt (46 km) or the Four-eye Butterfly Fish, *Chaetodon capistratus* (52 km; Puebla et al. 2012).

CONNECTIVITY, ESSENTIAL HABITAT AND MARINE RESERVE DESIGN

The results of this work have significant implications for our understanding of ontogenetic migrations, habitat use and their application to management. The general characteristics of ontogenetic migrations are summarized in Table 1. The ability to map habitat use across many species over ontogeny was itself a major step forward. However, comparisons among different studies and locations [La Parguera (Cerveny 2006, Aguilar-Perera and Appeldoorn 2007, 2008), Mona Island (Schärer et al. 2008), Biscayne Bay (Lindeman et al. 1998), Curacao (Nagelkerken et al. 2000a, Cocheret de la Morinière et al. 2002, Providencia (Appeldoorn et al. 2003)] further showed

that species patterns were similar despite large differences in the width of the shelf and the location and arrangement of habitat features, although some flexibility was apparent due to local differences (Appeldoorn et al. 2009). Thus, general rules concerning ontogenetic migrations could be developed and applied across a broad range of seascapes, especially those of variable shelf width (but see McMahon et al. 2016).

Another lesson is that the concept of essential fish habitat, while useful when thinking within species, may not be practical for management when viewed over all species because, essentially, almost the totality of habitats across the shelf are important to at least one species. While at least some protection for the whole of the marine environment is desirable, management needs to be able to prioritize the areas needing extra protection. This suggests that a more tractable view of essential fish habitat would be to use a multispecies approach, identifying areas where the diversity, amount, and distribution of habitats support the greatest diversity, and likely productivity (Duffy 2009, Gravel et al. 2011), of fishes; these hotspots are multispecies essential fish habitat (Cerveny et al. 2011). Identifying these immediately plays back on the use of marine reserves, and the criteria for identifying both are similar.

The basic biological principles of marine reserve design were specified by Ballantine (1997a, b): (1) representation – all community assemblages in each biological region should be represented; (2) replication – all community assemblages must be replicated; and (3) self-sustaining – the system should include all structural and functional components necessary to maintain itself, that is, areas should be linked in a network fashion. The object of management under this approach is habitat, recognizing that different habitats represent different communities (Sala

TABLE 2. Breakdown of habitat types to maximize ecological function from available data for Puerto Rico, based on community structure and function (From Appeldoorn et al. 2011).

Habitat	Description / Function
Reef	
Category:	
Colonized pavement (with/without sand channels) and Colonized Bedrock	Flat/low relief. Gorgonians, sponges, few corals
Linear Reef, Spur and Groove, Large Patch Reef	Large structures, high relief; include forereef, with some emergent
Small patch reefs and scattered coral	Small patches of reef, 1-3 m of relief within matrix of sand/algal plain
Location:	
Forereef	Windward margin of emergent reefs
Lagoon, Reef Crest, Shoreline intertidal	Shallow, associated with emergent reefs; settlement and nursery area
Back Reef	Associated with emergent reefs, deeper and more sheltered
Bankshelf	Outer shelf, 7-20 m deep; not associated with emergent reefs
Bankshelf Escarpment	Deep forereef at shelf edge
Seagrass (Location)	
Backreef and Reef Crest	Associated with emergent reefs; medium seagrass density; clean coarse sand; settlement and nursery area
Lagoon and Shoreline Intertidal	Shallow, dense seagrass; silty bottom and shelter areas
Deep Seagrass	Feeding ground
Mangroves (Location)	
Shoreline Edges	Coastal nursery habitat for reef fish
Mangrove Keys	Coral cay nursery habitat for reef fish
Coastal Mangroves	Habitat for prop root/lagoon fishes/nesting birds, etc.; export nutrients/biomass

et al. 2002, Aíramé et al. 2003, Leslie et al. 2003). For me, this represented a distinct and welcomed departure from single species stock assessment, where the focus is on populations. Protecting habitat is a key goal of ecosystem-based management (Appeldoorn 2008).

In practice the selection of areas for protection is complex due to the high number of ecological factors involved and potential for conflicting goals. Site selection, thus, involves a multivariable system where each element can be considered differentially according to local characteristics. Numerical models, such as Marxan (Possingham et al. 2000) can be used to realize these evaluations in an objective manner based on predetermined assumptions and goals. However, to meet basic design principles, model implementation requires that the available data (e.g., habitat types and distributions) and scale of analysis are structured so that the relevant ecology of the system is accounted for.

Knowledge of ecological connectivity can inform how to best meet design criteria. For this, it is convenient to divide connectivity into 2 relative scales: one dealing with ecological exchange among habitats within a local area (habitat connectivity), and another dealing with long-distance dispersal between areas (larval connectivity). Knowledge of habitat connectivity aids in defining habitats and the scale at which they are chosen. It also provides guidelines for assessing results. Larval connectivity helps inform the acceptable minimum distance between replicate target areas. Habitat distributions best serve as proxies for species distributions when the habitats can reflect, as closely as possible, the changes in community structure that arise from

subtle yet significant differences in habitat structure and from landscape effects. Thus, habitat types such as reef, mangroves and seagrass beds should be subdivided according to not only their structure, but their location within the larger habitat mosaic that affects species movements. We applied this approach to identify critical areas for management in Puerto Rico (Appeldoorn et al. 2011, Pagán et al. 2011) using Marxan and habitat data only, derived primarily from the NOAA/NCCOS habitat map (Kendall et al. 2001). In this, we partitioned habitat on the basis of habitat category and location, guided by our past work and others (e.g., Kimmel 1985). For example, reef habitat was partitioned into 18 types based on 3 categories and 7 locations across the shelf (Table 2).

Marxan works by minimizing the number of planning units needed to include the desired proportion (e.g., 30%) of each habitat. Considering that feeding migrations occur within hundreds of meters, we chose a hexagonal-shaped planning unit 1 km on a side (~2.6 km²). Short migrations would then occur within a single unit. This is facilitated by the defined habitat types; in attempting to minimize the number of planning units, Marxan will preferentially select planning units with multiple habitat types, thus insuring, for example, that adjacent forereef and backreef areas will be selected together, which in this case would accommodate adult White Grunt feeding migrations (Recksiek et al. 1991). Longer migrations may cross planning unit boundaries. Here, clustering is used to force Marxan to consider adding adjacent planning units. Clustering and defining habitat type on the basis of location aid in forming broader

TABLE 3. Criteria for assessing if area selection retains ecological function (modified from Appeldoorn et al. 2011).

Criterion	Metric	Connectivity Goal
Maximum spacing among clusters	40 km	Larval connectivity
Habitats included within cluster	All	High diversity & feeding migrations
Spatial extent of cluster	Coastline to Shelf edge	Ontogenetic migrations
Maximum habitat separation	102 – 103 m	Feeding migrations

areas that extend from the shoreline to the shelf–edge, which would account for ontogenetic migrations.

Marxan results are also evaluated by criteria set by connectivity concerns (Table 3). Comparing these to one Marxan run (Figure 6) shows that not all criteria were met. The program did a good job meeting the goals related to habitat connectivity, but large portions of the south and west coasts did not meet the 35km criteria (Appeldoorn et al. 2011) necessary for maintaining connectivity among selected areas. This is particularly acute for the case of Mona Island, a known partial geographic boundary (Taylor and Hellberg 2003) with limited connectivity to the western platform (Beltran et al. 2017), although habitats for the outer western shelf were not within the data used. Meeting the criteria for larval connectivity could be achieved by rerunning the analysis using the maximum distance constraint within Marxan, which specifies that selected areas cannot be more than a specified distance apart.

CONCLUSION

Why is connectivity everything? Pauly and Christensen (1995) estimated that 8.3% of the primary production in coastal and coral ecosystems is used to support fishing. While substantial, they further argue that this is potentially reduced by two-thirds from the value typical of tropical shelves because on the one hand coastal and coral ecosystems have a higher level of productivity, but on the other hand much extraction occurs at lower trophic levels (e.g., herbivorous mollusks such as conch and top

shells, but also parrotfishes and surgeonfishes) and there is substantial overfishing, such that the reduced biomass of exploited species is unable to use all the available primary production (cf. Guénette and Hill 2009). Current extractive and non-extractive (e.g., Hawkins and Roberts 1992, Barker and Roberts 2004) processes, coupled with threats from climate change and land-based sources of pollution are putting at risk the ecosystem services provided by healthy coral reef ecosystems (Moberg and Folke 1999). With such high rates of exploitation, and production potentially limited by external threats, fisheries management needs a more holistic, ecosystem approach (Appeldoorn 2008, 2011). Marine ecosystems are complex socio-ecological systems where managing for resilience should be a high priority (Hughes et al. 2005, Walker and Salt 2006). This approach and the maintenance of resilience is driven entirely by connectivity issues. While I have largely limited discussion here to aspects of spatial connectivity, trophic connectivity is equally important, as this relates to bottom-up versus top-down control of community structure and the potential impacts of the effective loss of keystone species. Considerations of fishing, which occurs at multiple trophic levels, must also include its drivers, which then includes other socio-economic and cultural connections (which I leave to the social scientists to elaborate).

Foley et al. (2010) identified connectivity as one of the core ecological principles that must be considered for marine spatial planning. This is easier said than done. For example, Klein et al.

FIGURE 6. Results of Marxan analysis, with target selection set at 30% of each habitat type. Best result of 200 iterations under a high cluster scenario ($cl = 0.005$). Selected planning units (hexagons) are in blue. Dashed line represents the edge of the insular shelf (50 m depth contour). Areas without hexagons had no habitat information. Modified from Appeldoorn et al. (2011).

FIGURE 7. Results of Marxan analysis, with target selection set at 30% of each habitat type, high cluster scenario ($cl = 0.005$), and 200 iterations. Colors represent the frequency that each planning unit (hexagon) was selected over the 200 iterations, with red = high and dark green = low. Dashed line represents the edge of the insular shelf (50-m depth contour).

(2010) used Marxan with Zones, with the goal of minimizing cost to fisheries, to model potential management areas off California under various scenarios. While their approach explicitly modeled the differential importance of specific areas relative to fishing effort, they did not do this for habitat. Rather they assumed all areas of a given habitat type have equal weight. As such, they did not consider the differential roles of habitat or their ecological importance as manifested through connectivity.

As argued above, I suggest that a first step would be to run Marxan using habitat data only, with that data being parsed as much as possible to represent different biological communities, including ontogenetic stages. Examining both the frequency at which planning units are chosen (Figure 7) and the areas subsequently chosen to optimally meet conservation goals and connectivity criteria (Figure 6) identifies critical hotspots within the overall ecosystem important for maintaining productivity. Clustering the outcomes over multiple Marxan runs (Aíramé et al. 2003) can offer some flexibility to this interpretation. This approach can then be used to scale the ecological importance of each planning unit, which could then be fed into a second Marxan with Zones analysis. The key point of this is that ecosystem productivity, and how it is structured spatially, is what supports all the activities we attempt to manage; thus any attempt at zoning must make sure that productive capacity is maintained. Metcalf et al. (2015) take this concept and extend it within a formal quantitative model for marine spatial planning that links Marxan with Zones to an ecosystem model (Ecospace, derived from an Ecopath with Ecosim model), to account for ecological processes and dynamics. Connectivity is explicitly included, as Ecospace calculates movement between adjacent cells as driven by processes such as foraging behavior, predator avoidance, and dispersal rates linked to specific habitat preferences. Their results not only predicted reduced impacts to stakeholders, but also illustrated the importance of both limited-take and no-

take zones when using spatial planning to achieve conservation and fishery benefits. While this level of quantitative modeling will be beyond the capability of many jurisdictions, their conclusions are generally applicable, and the more data-limited approach outlined above using just Marxan should provide a good approximation.

And, OK, maybe connectivity is not “everything”. There is still a significant role for traditional stock assessment. I have been fortunate enough to be integrally involved for over 20 years in the successful management of Jamaica’s industrial fishery for queen conch on Pedro Bank (Aiken et al. 2006), which now includes control rules based on biomass (density) targets. Yet, this is not a typical artisanal, coral reef fishery. More conventionally, the availability of data-limited methods (Newman et al. 2015) offers the hope that assessments within coral reef fisheries may be more routinely possible, especially given the current mandate within the United States for MSY-based quotas (Sagarèse et al. 2018). In the meantime, I would still contrast this with the success of several management measures within the U.S. Caribbean targeting spawning aggregations. Most notably, the initial seasonal closure of the Red Hind Bank and subsequent permanent closure of the larger Marine Conservation District in the U.S. Virgin Islands led to a recovery of both the spawning population of Red Hind (Nemeth 2005) and the underlying population, increasing the mean size in the catch. This success is based on 2 aspects of connectivity: the ability to target management spatially because of the spawning migration and aggregation of the species, and the dispersal (spillover) of larvae and adults from the closed area. While there has been substantial effort on assessing the magnitude and extent of connectivity in marine populations, there remains much to do (Bryan-Brown 2017). Yet, the rationale for incorporating connectivity into management is well established in both theory and practice, and there exists a sufficient number and variety of applications to

demonstrate how this can be achieved under various conditions of management capacity and resource knowledge.

So, connectivity is everything. Now, if climate change doesn't change everything.....

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