Chapter 7
Aggregation Spawning: Biological Aspects of the Early Life History

Patrick L. Colin

Abstract Most reef fishes have bipartite life histories, separate pelagic-oceanic (egg/larvae) and benthic (juvenile/adult) periods. The several-week pelagic period has early planktonic (egg, yolk sac and preflexion larva) and later nektonic components (post-flexion larva to settlement); the plankton-nekton transition timing is variable. For aggregating species, larvae are weak swimmers early in life, but late stages are often strong swimmers able to perhaps influence their settlement locations. No obvious differences were found between larval stages of aggregating and non-aggregating species and both types of spawning are found within single families, and even within a species. There are no egg types, morphologies, feeding strategies or special structures exclusive to aggregating species. Initial dispersal is determined by location and time of spawning. Pelagic eggs are buoyant, keeping them in near-surface waters and away from benthic predators. The larvae go through a series of stages (egg, yolk sac larvae, pre- and post-flexion larvae, pelagic juvenile), becoming larger and more capable over time. Critical periods occur and can cause major mortality of a cohort. Ocean conditions during the early egg and yolk sac stage are critical to survival followed by initiation of feeding as a second critical event. During pelagic life larvae must survive in open water, find appropriate food as larvae and avoid predators. Cohorts from aggregations can recruit as a large pulse, but other fishes may also have such pulses. The mass spawnings of reef invertebrates, such as stony corals, are generally not comparable to those of fishes, while crustaceans (spiny lobsters, marine crabs, terrestrial crabs) have some similarities. There is a need for fisheries oceanography research on aggregation spawning, as well as more work on laboratory culture. The question of potential maternal benefits to larvae needs careful attention.

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7.1 Introduction

During their early life history (ELH), which covers the period between spawning and settlement as juvenile fishes from the water column, reef fish larvae must survive and grow in the pelagic environment in order to successfully recruit to the benthic stage. Chap. 6 examined the physical and biological environment impacting the dispersal and retention of reef fish larvae, emphasising those with aggregation spawning. This chapter examines the biology of reef fish larvae from spawning through metamorphosis to try to (1) discern any intrinsic differences between aggregation spawned and other reef fish larvae, and (2) determine the common features of larval development across those families with at least some members engaged in aggregation spawning. Basic information is first provided on the morphology of larvae, the probable critical periods in ELH, then examines what differences and similarities exist between species in their spawning behaviour and initial dispersal, and how predators might affect success of spawning. Comparisons are made with potentially similar broadcast spawners and future research directions are indicated.

The larvae and the juveniles/adults of reef fishes occupy very different habitats, the former generally in open water "pelagic" environments and the latter in benthic or near benthic habitats (Fig. 7.1). On an individual basis the ELH of aggregation spawning reef fishes seems essentially identical to those reef fishes lacking aggregation spawning. The same determinants of survival (feeding, predation, transport, water quality) operate on all larvae. If differences do exist, they might provide some insight into the reasons why some fishes engage in aggregation spawning. While considerable progress has been made in understanding the early life history of reef fishes in general (reviews include Cowen and Sponaugle 2009; Leis and McCormick 2002; Cowen 2002), attention has been focused more on species with demersal eggs and short larval lives. Settlement-stage fishes can be captured in good condition using light traps and other means. Some studies utilize cultured larvae, again mostly from families with demersal eggs, which are easier to culture. The understandable attention paid towards the more easily studied species has resulted in a tendency to consider all larvae to behave similarly and to not appreciate the vast differences between early and late stage larvae.

While it is often feasible to investigate ELH at its start (spawning or hatching) and its conclusion (settlement), when fishes are near reefs or other shelf areas, the period of weeks between is not easily examined. The numbers of larvae in the open ocean are generally low relative to the water volume, and deciphering the pelagic life of reef fishes is not easy, usually requiring costly shipboard work followed by tedious sorting and identification. Our rudimentary knowledge severely limits the understanding of what affects success of a given cohort of fishes.

Questions about whether eggs/larvae from a large mass spawn stay together for extended periods of time (until at least time of first feeding) have been examined in the previous chapter, and the initial answer seems to be a qualified "no". The physical mechanisms operating at these early stages generally favour gradual dispersal away from the location of spawning, with perhaps only the slight buoyancy and later vertical movement ability of yolk sac larvae to promote concentration along oceanic fronts.

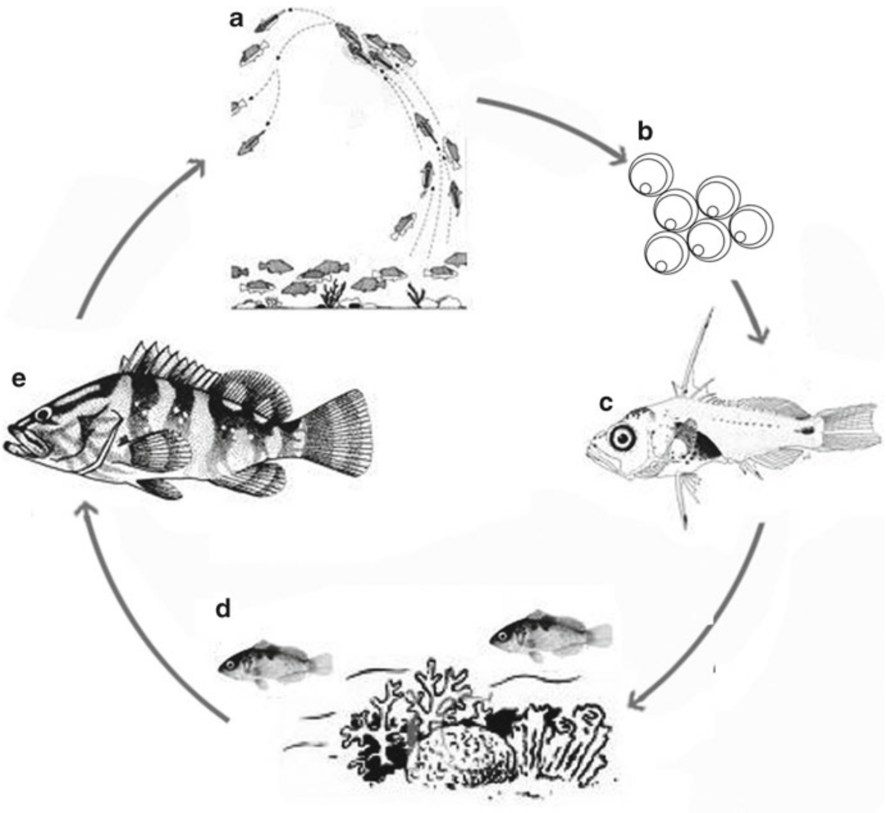

Fig. 7.1 The bipartite life cycle (pelagic eggs and larvae with benthic juveniles and adults) of most reef fishes is shown here, using the Nassau grouper as an example. (**a**) Spawning, in this case from an aggregation, produces (**b**) small fertile eggs which drift away with the current. (**c**) Larvae develop over several weeks in the pelagic environment and (**d**) eventually settle to take up benthic life as juveniles. (**e**) Over time, usually a number of years, fish grow to become mature adults which spawn to start the cycle again (Figure: Yvonne Sadovy de Mitcheson with permission)

Aggregation propagules do not, apparently, form a cohesive group that would remain so in the pelagic environment. So does aggregation spawning provide any benefit to early larvae? That question is still open, but may be examined by seeing whether or not the conditions at times of aggregation spawning might promote success of larvae through recruitment, particularly if other larval components are present which might compete with fish larvae.

Reef fish eggs and larvae initially act as drifting plankton, and at a later stage some become capable of behaving more as free-swimming nektonic organisms (Leis 2006). The exact stage of transition between the plankton-nekton, when larvae go from being passive drifters to active swimmers, is variable. The extent to which late stage larvae use sensory means to navigate or seek out settlement locations is an area of considerable research, but also of much uncertainty. Larvae normally differ greatly in morphology from juveniles/adults of the same species and have fewer morphological characters to assist with identification. Often it is impossible to identify larvae to species (particularly early stages). Placing them into a genus or family can be difficult, inhibiting many types of ELH research (Leis and McCormick 2002). Leis and Rennis (1983), Leis and Trnski (1989) and Leis and Carson-Ewart (2000) provide available taxonomic information on many shallow water Indo-west Pacific (IWP) ELH stages while Richards (2006) has done so for the western Atlantic (WA) region. Other methods, such as use of otolith increments and chemistry, have allowed new perspectives on ELH.

7.2 Taxonomic Range of Aggregation Spawning

Both aggregation and non-aggregation spawning occur within various families of reef fishes and their eggs and larvae do not appear to differ markedly among co-familials according to spawning strategy (see Appendix) (see also Chap. 4). Aggregation- and pair-spawning by related species (and even within a single species in some wrasses-Labridae and parrotfishes-Scaridae) often occur simultaneously on the same reef area, their eggs mixing in open water. Whether there is anything different or beneficial for ELH between aggregation and non-aggregation spawners is uncertain but nonetheless central to the question of why aggregation spawning exists at all. It appears at the time of first feeding that the density of larvae in the open ocean from a very large aggregation spawning may not be significantly higher than for other types of spawning (see Chap. 6). Once they start feeding a few days after hatching, how larvae can be sustained by the generally low zooplankton populations found in most tropical waters is crucial. Chapter 6 indicated some biophysical mechanisms that potentially concentrate the larvae, the food items they need and potential predators. Other mechanisms might reduce the density of larvae through predation and dispersal so they become less concentrated.

7.3 Early Life History Stages of Coral Reef Fishes

Most fishes with spawning aggregations have planktonic eggs. A limited group of aggregating species has eggs which develop on the bottom (see Appendix) and whose dispersal and pelagic life does not start until hatching. Knowledge of larval stages and behaviour usually comes from capture of specimens using plankton nets, light traps and other techniques, as well as rearing of eggs in culture. Some *in situ* studies are being undertaken, mostly with settlement stage fishes (Leis et al. 1996, 2003; Paris et al. 2008). The ELH stages of aggregating fishes are typical of other reef fishes, and those stages can be broken down as follows:

Eggs (pelagic) – These can be of variable shape, but most often nearly spherical; typically ranging from about 0.6 to 1.2 mm diameter; larger for eels (up to 4 mm), and some non-perciform groups like *Fistularia* and tetradontiforms. Some parrotfishes have distinctive spindle-shaped eggs up to about 2.5 mm long and 0.5 mm wide. Most free-spawned eggs are slightly buoyant, nearly transparent, with yolk and oil globule(s), as well as a hard outer chorion. The yolk provides food for the embryo in the egg and yolk sac larva stages. The oil globule may contain materials, such as triacylglycerol (TAG) lipids, important for larval nutrition. Most pelagic reef fish eggs hatch within 24 h to yolk-sac larvae. Species with negatively buoyant, adhesive, small eggs (triggerfishes-Balistidae, rabbitfishes-Siganidae) also hatch quickly. Eggs attached to the bottom or other objects (damselfishes-Pomacentridae) are generally larger, not spherical, take longer to hatch and are ready to feed within hours of hatching.

Yolk sac larvae – Pelagic eggs at hatching are essentially embryos attached to the large yolk sac, often with slight positive buoyancy, and have very limited swimming ability. Over a few days they develop functional eyes, a complete gut with mouth and anus, rudimentary fins and nervous system. The benthic eggs of triggerfishes and rabbitfishes quickly hatch into larvae similar to those with pelagic eggs. Others with demersal eggs (e.g. damselfishes) go through the yolk sac stage in the egg capsule for some days and at hatching are capable of weak swimming and ready to feed quickly. Most fishes with demersal eggs do not aggregate for spawning. Otoliths (ear bones) begin to develop in the yolk sac stage.

Early stage larvae (preflexion) – Pelagic larvae initiate feeding on external foods once the systems necessary (complete gut, pigmented eyes, ability to orientate) have been developed during the yolk sac stage. Larvae possess a notochord without any caudal fin supporting structures. The nearly transparent bodies of early larvae, an adaptation to pelagic life, have the body musculature divided into myomeres, which have a near one-to-one correspondence with the eventual number of vertebrae. Pigment is often limited to the eyes, over the gut area and as scattered chromatophores or melanophores on the body. There is a medial fringe of thin tissue, the fin fold, around the posterior end which becomes differentiated into the medial fins. Rudimentary pectoral fins are usually present. A swim bladder may form and usually inflates some days after the larvae start to feed, reducing negative buoyancy. The otoliths develop with rings being laid down which allow for age determination, if the rings are formed daily or at another known interval, since otolith formation.

Late stage larvae (post-flexion) – As larvae grow, the posterior end of the notochord flexes upward in the process called “flexion” establishing the location where the supporting elements of the caudal fin will develop. Once flexion is complete, the larva is in the “post-flexion” stage. Formation of caudal fin supporting elements occurs over time and the vertebrae develop. Larvae often become more pigmented, and develop specialized structures in some families (some may start prior to flexion). Swimming ability is greatly increased once the caudal fin is developed. The larval stage is considered to end when all external meristic characters (fin spines and rays, etc.) develop and temporary special features for pelagic life are lost.

The pelagic juvenile stage – Still living in open water, they have nearly the full morphology of the benthic stages, but usually are partially transparent and lack the benthic juvenile colour pattern. The pelagic juvenile stage (also called "pre-settlement") may persist for some time if a suitable settlement environment is not found. Pelagic juveniles are usually ready to settle from the plankton and take up benthic life.

The benthic juvenile stage – The young fish takes up life on the bottom and quickly acquires normal juvenile coloration. Any adaptations for pelagic life are quickly lost. This stage is also termed "post-settlement".

7.4 Dynamics of Life History Stages and Events

Aside from the developmental stages, there are a number of critical life history events during pelagic life, and failure to transition through these results in high mortality of a given larval cohort. ELH for all reef fishes can potentially be divided into early, middle and late stages. The early starts at fertilization, ends with the initiation of notochord flexion and can be characterized by multiple critical events, including first feeding and swim bladder inflation. During the middle stage the caudal and other fin supporting elements become complete, some specialized structures (which potentially enhance survival) become fully developed, and significant vertical movements in pelagic environments may occur. Rapid growth during this stage appears to be important in eventual success in recruitment and early benthic life. The late stage (also termed the "settlement stage") starts at the transition to a pelagic juvenile, loss of specialized structures, enhancement of swimming ability and the potential to use sound, olfactory or other cues to navigate towards suitable settlement habitats, followed by settlement to a benthic existence. During all stages larvae are moving, either by drifting or by actively swimming (and navigating?), and may be selecting a given depth, perhaps on a diel schedule. Once ready to feed, they need to do so continually (with interruptions at night?). The negative consequences of failing to do so are probably more important in the early stages. They must avoid predators at all times.

7.4.1 The Start of Pelagic Life – Aspects of the Early Stages

After spawning, egg and yolk sac larva mortality can potentially be high if conditions of turbulence, salinity, temperature and light are unsuitable, as demonstrated in culture studies. Ellis et al (1997) reported that low turbulence, high light and high salinity were optimal for survival of larval Nassau grouper, *Epinephelus striatus*, from hatching to first feeding. Increased survival under high versus low (to zero) light intensity points to possible relationships between light intensity (affecting behaviour through phototaxis and swimming activity), diel timing, and size at first feeding, which may extend throughout ELH. Finally, larvae in completely static water had a less than 1% hatching success suggesting that exceptionally calm seas could have a negative effect on hatching. While this study and others (Akatsu et al. 1983; Watanabe et al. 1995, 1996, 1998), have been conducted in rearing tanks rather than under natural conditions, they demonstrate that such factors may influence survival in the field. Unpredictable weather conditions may result in spawning under less than optimal conditions and result in failure of a cohort spawned in an aggregation. Certainly cohort size can vary considerably in aggregating species. For example, in the leopard coralgrouper, *Plectropomus leopardus*, a single cohort was found to dominate in areas closed to fishing on central the Great Barrier Reef, Australia (Russ et al. 1996).

First feeding – If physical conditions are acceptable, the critical transition from yolk feeding to capturing food can occur. Larvae ready to begin feeding lack a caudal supporting structure and other well-developed fins; however they can swim in a coordinated fashion to orient, approach and strike at potential food items. They are not capable of swimming well enough for migration purposes, have limited ability to control their depth and often lack an inflated swim bladder. It seems likely that early feeding of aggregation-spawned reef fish larvae will be dependent on vision for feeding and limited to periods of adequate daylight. At first feeding the larvae capture food items usually by launching themselves at the food item and ingesting it. Within few days feeding ability develops so they can feed by striking forward using the pectoral fins or an "S" or "C" shaped bend in the body, and engulfing prey with, by now, protrusible jaws.

If the correct type and size of food organisms are present and feeding is initiated (a "match") survival may be high, or if the larval state and food available are incorrect (a "mismatch") the larvae face starvation in a very short time period. This "match-mismatch" hypothesis (Sinclair 1988) has been widely accepted from studies of temperate ichthyoplankton, and is undergoing some revisions to thinking as more information becomes available (Leis and McCormick 2002). Almost certainly the limited time between exhaustion of the yolk and starting to feed externally is a "critical period" but the time limits are poorly known for reef fish larvae. The times of hatching and exhaustion of the yolk after spawning are dependent on temperature; higher temperatures producing shorter time spans. For larvae of cultured Malabar grouper, *Epinephelus malabaricus*, for example, Yoseda et al. (2006) found the volume of yolk remaining, representing endogenous energy reserves at time of opening of the mouth and the onset of feeding, to be higher at 25°C than at 28° and 31°C. By delaying the start of feeding by 6–24 h after mouth opening, they found only a short period where this delay did not affect survival. Overall the higher the energy reserves remaining when feeding can begin, the greater the chance of successfully transitioning to exogenous food. Some results seem contrary, however. For example, Sugama et al. (2004) reported highest survival of highfin grouper, *Cromileptes altivelis* (Serranidae), larvae at 28°C (versus 25° and 31°C) although larvae, fed rotifers (density of 5–10 per litre), held at 31°C ingested more rotifers and had higher growth rates.

Inflation of the swim bladder – Most reef fishes with pelagic eggs, including aggregation species, have swim bladders as juveniles/adults which develop during larval life.

The point at which the bladder becomes functional (gas-filled) is considered "inflation" and can represent another "critical period". For some larvae it is believed they must rise to the surface to ingest air (Czesny et al. 2005). In some living larvae the swim bladder is visible as a silvery structure over the gut due to their generally transparent nature; however the swim bladder is often masked by melanophores and not always visible externally. Once inflation has occurred, the larvae may change from negatively to neutrally buoyant, this change apparent in the angle at which the body is held in the water. Data on time of inflation are sparse, but, for example, in the red grouper, *Epinephelus morio,* it was observed at 12 days post-hatching (Colin et al. 1996) and Drass et al. (2000) observed it 4–6 days post-hatching in 2.4 mm notochord length (NL) reared larvae of the red snapper, *Lutjanus campechanus*.

Flexion – Swimming of sufficient speed and duration to match ambient currents is nearly impossible for early larvae. Prior to flexion, swimming is adequate for food capture and perhaps to change depths to a limited degree, but not to migrate any distance. During their early stages larvae might be concentrated by mechanisms, such as by maintaining a given depth along a descending front, but may not actively seek such mechanisms. Their swimming ability might allow them to remain, once encountered, with high concentrations of food. While flexion is easily noted in larval specimens, the age of its occurrence is often not known for field-caught specimens. Rearing studies provide some indication that it may occur roughly half way (or more) through the larval life. For example Clarke et al. (1997) reported notochord flexion in several species of snappers (Lutjanidae) to start at 11–12 days post-hatching and to be complete at 16–18 days, while metamorphosis occurred at ages of 22–33 days. For red grouper Colin et al. (1996) found flexion to occur at about 16 days, with a total pelagic life of 35 days.

7.4.2 Are There Differences in ELH Between Aggregation and Non-aggregation Spawners?

Fish families with aggregation spawning also have non-aggregating species. Within these families the larvae of the two spawning types do not appear different and the requirements to promote survival to recruitment are probably similar. Are there, however, possible differences in egg type or size for fishes with different strategies? Are all propagules equivalent? For egg types, it seems unlikely that differences exist. If a family has two egg morphologies (e.g. spherical versus spindle in parrotfishes), they are found for both types of spawning. Where dual modes of spawning (pair- and group-spawning) exist in one species (e.g. parrotfishes and wrasses), the eggs produced are also identical, or nearly so, and individual females may alternate between pair and group spawning. Robertson (1996) did report a 5% higher egg volume in group-spawned versus pair-spawned eggs of *T. bifasciatum*. This represents a difference of less than 2% in diameter and may represent a slightly different degree of hydration.

However, egg size differences may be uncorrelated with adult fish size and vary geographically or seasonally. For spherical eggs, small differences in egg diameter produce greater differences in egg volume which consists largely of yolk. A 26% increase in diameter results in a doubling of egg, and presumably yolk, volume. Some large reef fishes have small eggs; the humphead wrasse, *Cheilinus undulatus*, and bumphead parrotfish, *Bolbometopon muricatum*, the largest members of their families, have hydrated eggs averaging only 0.66 and 0.65 mm in diameter, respectively (Colin 2010; Bell and Colin 1986). The Micronesian wrasse, *Labropsis micronesica*, a non-aggregating wrasse reaching less than 100 mm SL, has a 0.80 mm diameter egg, twice the volume of a humphead wrasse egg. In the Atlantic its largest wrasse, the hogfish *Lachnolaimus maximus* (a possible, but unverified aggregator), has eggs 1.2 mm in diameter (Colin 1983) while eggs of the bluehead wrasse, *Thalassoma bifasciatum* (reaching about 150 mm SL), with dual spawning modes, are about 0.56 mm in diameter (Holt and Riley 1999). While the egg of the hogfish is quite large, the eggs of most other Atlantic species seem similar to comparable Pacific species (Richards 2006).

For the eggs of a single species, the influence of maternal age and condition may determine the quality of eggs and subsequent survival/growth of larvae. The "provisioning" of larvae with energy-rich TAG lipids (found largely in the oil globule) increased with female age in black rockfish, *Sebastes melanops* (Scorpaenidae), and correlated with subsequent growth and survival (Berkeley et al. 2004). For reef fishes the importance of egg quality is known for some damselfishes with demersal eggs (reviewed by Leis and McCormick 2002), although little is known for those with pelagic eggs. In damselfishes maternal hormones and nutritional components incorporated into egg yolk, the size of eggs and the size of larvae at hatch are affected by feeding conditions of the female and behavioural interactions with conspecifics. The larvae resulting from such "superior" eggs grow and develop faster reducing time spent in the pelagic environment, thereby reducing the potential for mortality of a cohort. It has been shown for species of surgeonfish (Bergenius et al. 2002) and wrasse (Grorud-Colvert and Sponaugle 2006), both species with aggregation spawning, that fast early growth can have positive effects on recruitment success.

The role of social factors in spawning aggregations (with the possible exception of sex change) is unstudied. It is conceivable that aggregations provide abundant opportunity for adults, particularly females, to be influenced by their interactions with conspecifics through hormonal actions and increased "quality" of their eggs, similar to the effect identified in damselfishes or through sexual selection and mate choice (McCormick 1998, 1999a, b; McCormick and Nechaev 2002, Chap. 3). For transient aggregators (TAs), who often have their reproduction limited to a few short periods each year, if social interactions and hormonal effects can improve "quality" of eggs produced, their relatively short spawning season may also help to maintain egg size and quality (as opposed to long spawning seasons when egg quality may decline over time, Leis and McCormick 2002). It would be important to know if the nutritional fitness of the ova is determined by feeding activities prior to any migration, which might take several days during which feeding may not occur, to evaluate the benefits to egg quality when a transient aggregator then undertakes a significant migration prior to spawning. Groupers at transient aggregations are known to feed between lunar spawning periods, perhaps to maintain nutritional fitness and egg quality (see Chap. 2).

Social factors, perhaps increasing the survival of transient spawned larvae, might provide reasons for the evolution and maintenance of aggregating behaviour. If the larvae of transient aggregators, whose individuals often go through long migrations and elaborate preparations for spawning, are inherently superior compared to non-aggregating species, it might help explain why aggregation spawning has evolved in such species. The "stage duration" hypothesis "that larvae that grow and develop faster have higher survival and enhanced recruitment" (Leis and McCormick 2002) has support from studies of temperate and tropical species (Bergenius et al. 2002; Sponaugle and Pinkard 2004; Sponaugle et al. 2006). Studies of hormone and nutrition levels in adult females and in ova produced, both during ovulation and after spawning, are needed of both aggregating and non-aggregating species, perhaps from single families, to test whether aggregating species show particular benefits.

7.4.3 Spawning and Gamete Release

While maternal condition may increase growth and survival, potential benefits at the start of ELH may accrue from aggregation spawning when the environmental conditions are beneficial to the larvae. This might involve release into patches of water having specific properties conducive to larval survival (food in the form of zooplankton?), dispersal and retention. What little is known about the ocean dynamics related to the release of large numbers of propagules into a limited volume of water over short time periods was considered in Chap. 6. Some information on the biologically mediated dynamics of aggregations (food, predation) is provided here.

The overall movements of fishes engaged in the release of eggs and sperm in "free-spawning" reef fishes has been given various descriptive terms – rush, burst, dash, ascent, spawning run – and is the start of the process of early life history. Fishes present in aggregations spawn in three manners; as individual pairs (pair-spawn), as small groups that briefly break away from a larger aggregation (group-spawn), or in a single group comprising most individuals in the aggregation (mass spawn). Fertilization occurs quickly (within 1 min or so), unlike in many broadcast spawning invertebrates, and in most cases the vent areas of males and females are in very close proximity when gametes are released (Colin 2010), presumably increasing egg-sperm contact. Available data indicate that fertilization rates are generally quite high (90–100%) for many pair- and group-spawning species (Kiflawi et al. 1998). The massive sperm clouds released by some transient spawners (such as Nassau grouper, cubera snapper – *Lutjanus cyanopterus* and leopard grouper – *M. rosacea*) and high associated gonadosomatic indices of their males suggest in such cases that virtually all healthy eggs get fertilized (Colin 1992; Sala et al. 2003; Heyman et al. 2005). This may not be the case for some smaller pair spawning reef fishes (Petersen et al. 1992) and sperm limitation may occur (Petersen et al. 2001).

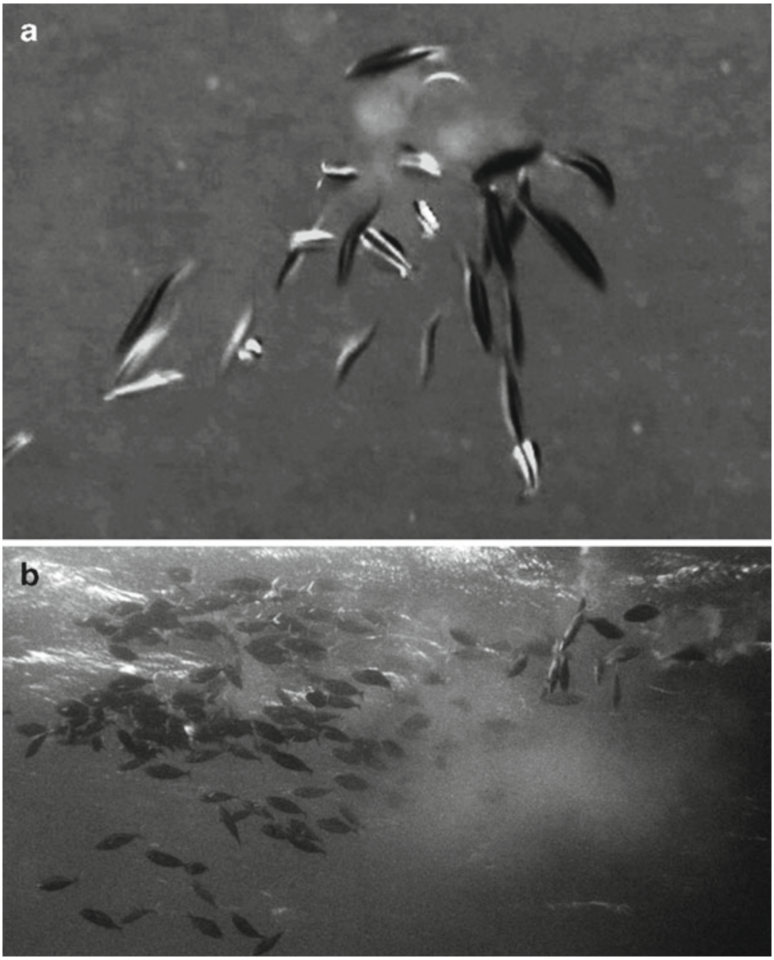

Fig. 7.2 (**a**) A relatively small gamete cloud is released by blunthead wrasse, *Thalassoma amblycephalum*. (**b**) Aggregation spawning by yellow and blueback fusilier, *Caesio teres,* produced a large gamete cloud easily visible due to the large amount of sperm released (Photos: Patrick L. Colin)

The nature of gamete release is related to depth of water over the reef. Where the depth is 5–10 m or more, the fish ascend to release eggs and sperm as a "burst", often spherical in shape. The group of fish follow a single ascending female (Figs. 7.2 and 7.3c), some taking inward radial paths, and sometimes spiral as a group, to release the gametes at a central point or along the spiral. Heyman et al. (2005) suggested that this spiralling might assist in propelling the eggs towards the surface after release. After release spawning fish radiate outward, usually descending towards the bottom (Fig. 7.2a). Spawn ascents that start with only a few fish are often joined by additional individuals within seconds. If the later arrivals are somewhat

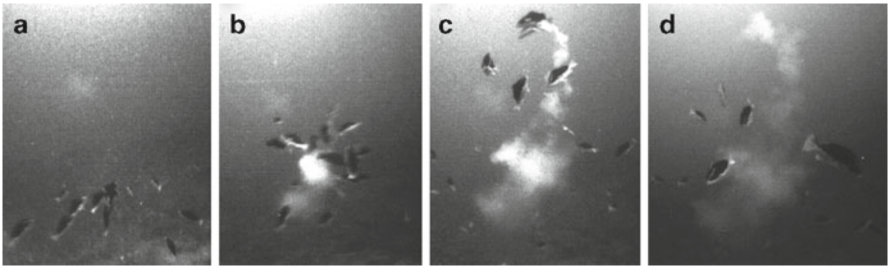

Fig. 7.3 The Nassau grouper, *Epinephelus striatus*, produces a highly visible gamete cloud when spawning, largely due to massive amounts of sperm being released. (**a**) A mix of males and females follow a single leading female prior to release. (**b**) The fish come together, release gametes in a limited volume of water, and then radiate outward. (**c**) In this case, a pair of Nassau grouper swam through the area of the gamete burst, continued upward and released gametes above the initial cloud. The male was streaming sperm, leaving a visible track of its path upward prior to spawning. (**d**) A few seconds after spawning the fish have all moved outward from the site of gamete release and the cloud is gradually starting to become less visible as it dissipates (Photos: Lori J. Colin)

behind the first group, their gamete release may not be in precisely in the same location, but close enough to the already present gametes that this usually serves to expand the overall size of the gamete cloud for a single spawning event. In some larger species, such as Nassau grouper (Fig. 7.3) and cubera snapper, there can be a succession of several gamete releases as fish rush in to join an initial group and start spiralling upward towards the surface, not breaking off quickly after the initial release (Heyman et al. 2005). In mass spawning, the entire mass of fish ascend, often slowly, then at the peak start swirling and releasing gametes, continuing for many seconds (Fig. 7.2b), and is seen in the spawning of yellow and blueback fusilier, *Caesio teres* (Bell and Colin 1986).

There can be variations on this general sequence. In one instance a group-spawn by Nassau groupers was followed just a few seconds later by a single pair (apparently male and female as only one fish was spewing sperm) which arched through where the group had already released and continued in an upward trajectory (Fig. 7.3). While unusual (it was the only such spawning I observed, photographed or recorded on video) it does indicate that more than one female might participate in a given spawning rush. For some large transient aggregators, when there are a series of individuals spawning near simultaneous bursts over the area of the aggregation, the individual spawns appear to merge to form a single large massive gamete cloud.

It is usually difficult to see the gametes when released. Eggs are nearly transparent, and only when copious are the sperm visible. For most pair and small group-spawning fishes, the gametes appear as a faint burst of particles in the water at the apex of a spawning rush which quickly diffuses and disappears (Fig. 7.2a, Colin 2010). Males of some of the larger transient aggregating species have large testes and their sperm can be seen as milky clouds in the water for a few minutes presumably because they release so much sperm at one time (Fig. 7.3).

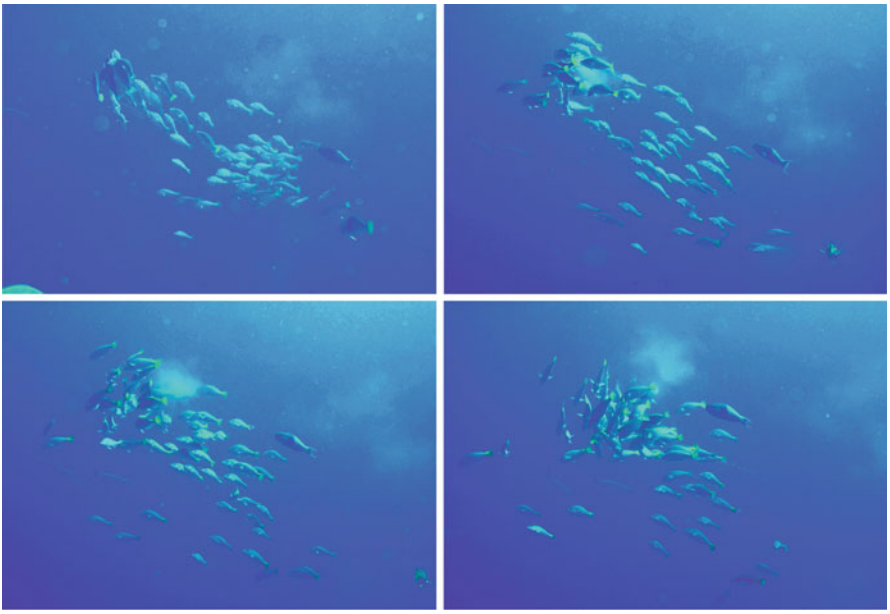

Fig. 7.4 Aggregation spawning by the longnose parrotfish, *Hipposcarus longiceps*, on the western barrier reef of Palau. Elapsed time is shown in the *upper right corner* of each photo. A single male redlip parrotfish, *Scarus rubroviolaceus*, is seen on the *right side* and had no involvement in the spawning activity (Photo: Patrick L. Colin)

If water depths are shallow (only a few metres) and the expanse of an aggregation large compared to the depth (many 10's of metres across), multiple groups will make short spawning ascents from over the entire aggregation area, producing a flurry of spawning which leaves a large area of water with a visible gamete cloud. This is particularly seen in those IWP resident aggregators, typically surgeonfishes and parrotfishes, spawning on lengthy shallow fore reefs just after high tide (Hamner et al. 2007). Such a "broad launch" is often seen in surgeonfishes and parrotfishes (Fig. 7.4a), and can result in a band of gametes being carried off the shallow reef, rather than single gamete clouds, with current from the falling tide for roughly an hour (Hamner et al. 2007).

Other resident aggregators, such as bluehead wrasse, outside of tidally influenced areas, may have a series of individual spawning bursts transported sequentially away from the spawning site by whatever currents exist. Appeldoorn et al. (1994) tracked water masses found at multiple spawning sites of bluehead wrasse, and also at similar non-spawning sites on the same reef. They found transport away from the start site to be greater for releases at non-spawning sites, while there were no differences in broadscale transport within the reef tract. They found that patches from sites tended to merge during the 24 h period of observations. In the same area

Hensley et al. (1994) found that bluehead wrasse tended to group-spawn at sites that potentially offer advantages for off-reef transport of eggs, however, the benefits were only evident over the short term.

Nearly all pelagic reef fish eggs are very slightly positively buoyant after fertilization (see Chap. 5) and this buoyancy is helpful in keeping them in the water column where they can be dispersed and advected away from predators. Under extremely calm conditions eggs might rise and rest upon the water surface, something that happens in aquaria, and potentially exposes them to incident UV radiation. Some temperate fish eggs are known to have UV blocking compounds (Chioccara et al. 1980; Plack et al. 1981), but these have not been investigated for tropical reef fish pelagic eggs. Hamner et al. (2007) found that, for pelagic eggs (largely surgeonfishes, parrotfishes and wrasses) spawned near the surface at a site 80 m downcurrent and about 10 min after spawning, 90% of eggs were in the top 4 m of the water column with 60% of these in the top metre. On windy days with surface waves, fish eggs and zooplankton flowing off the reef would mix deeper, with greater under-sampling if plankton nets are moored at the surface.

7.5 Life in the Pelagic Environment – Aspects of the Middle Stage

The middle phase of ELH is characterized by an increase in swimming ability, which allows easier control of vertical distribution, necessary for selection of depth during a daily cycle, and food capture to maintain rapid growth to increase survival. Armsworth (2001) points out that, if possible, it is much more efficient to use vertical changes in position to move into water layers where advection will carry a larva towards a "desired point" than to actually swim the entire distance toward that point. The increased swimming ability is a result of swim bladder inflation, development of caudal supporting elements, and increasing development and strength of fins. There is also greater ability to avoid predators through growth of anti-predator structures (fin spines, head and body spination) and better swimming. Finding enough food consistently is a critical factor, both for fast growth and to prevent starvation as food reserves are slight. Schooling is unlikely. There is ample evidence of shifts in vertical distribution of larvae between day and night, with nocturnal periods characterized by shallower distributions. Vertical distributions can also modify dispersal trajectories.

7.5.1 Development of Specialized Structures

Specialized structures in larval reef fishes include elongate dorsal, anal and pelvic fin spines, elaborate head spination, and fin-rays with bulbous growths, with such structures limited to a single or a few families. Specialized growth includes highly compressed, high dorsal-ventral aspect (deep-bodied) and very elongate, larval form (leptocephalus) and often such larvae have been given distinctive names, sometimes based on initially erroneous descriptions of them as separate genera (acronurus, tholichthys). Specialized larvae and structures are found in many families with aggregation, in both aggregating and non-aggregating species of those families. Structures, such as spines (epinepheline groupers – Colin and Koenig 1996, surgeonfishes – Randall 1961), may serve in predator deterrence, but the functional use of these features is usually not apparent from studies of preserved specimens. For example, the dorsal and pelvic fin spines of epinepheline groupers form early (starting as soon as 7 days post-hatching at a preflexion notochord length of only 3 mm) and grow rapidly, reaching their maximum length in another 7–10 days at 6–7 mm NL (Colin and Koenig 1996). The spines are quite motile, can be erected nearly vertical and their ends clearly marked with dark melanophores. Their normal positions and angles combined with the location of the snout form a tetrahedron, presumably presenting potential predators with a greatly increased effective size of the larvae. Other examples of specialized structures occur in surgeonfishes; a highly compressed deep body, nearly as deep as long, with formidable dorsal and anal spines which increase its effective size. Once the caudal peduncle spine forms (at about 17 mm TL) the larvae is called an “acronurus” until settlement and metamorphosis.

Body form, without spines or other hard structures, may be modified. The leptocephalus is an elongate flattened leaf-like larva found in eels (order Anguilliformes) and a few primitive bony fishes, such as bonefishes and tarpon (order Elopiformes). Some elopiform fishes may spawn in aggregations. Bonefishes (Albulidae), for example, are reported to migrate through channels to spawn on outer reef slopes, although they may engage in simple migratory spawning rather than aggregate. At least one moray eel aggregates near the reef to spawn (Thresher 1984; Ferraris 1985).

7.5.2 *Growth and Feeding of Mid-stage Larvae*

While much of the larval life between the transport immediately after spawning away from the site and eventual appearance as recruits weeks later is largely unknown, some recent techniques provide tools to examine this life period. The occurrence of rings laid down, near daily, in otoliths of larvae has allowed precise ageing of many species, while the chemistry of otoliths, particularly the presence of stable isotopes, can indicate whether larvae have grown up in oceanic or near shore environments (Patterson et al. 2005). Hamilton et al (2008) used the occurrence of lead isotopes in otoliths of *T. bifasciatum* to distinguish larvae which developed in offshore (about 55%) and nearshore (about 45%) waters and followed their survival during the first month of benthic life which suggested different larval histories suffered differential mortality. Patterson and Swearer (2007) used elemental signatures in otoliths to attempt to identify natal locations for an endemic and a widespread species of wrasse with some success.

Llopiz and Cowen (2009a, b) found in the Straits of Florida high incidences of food in guts of larval fishes, including many from families with aggregation spawning, and a surprising diversity of feeding strategies, based on gut contents. Rapid gut evacuation and no evidence of nocturnal feeding was prevalent in scombroid larvae (based on sampling larvae after sunset) and it is likely reef fish larvae from these waters do the same. However the possibility exists that some reef fish larvae might be able to feed if in shallow water on nights with a near full moon as this provide considerable illumination in shallow water.

Interestingly Miller (2009) suggests that leptocephali larvae probably feed on particulate matter in the water column, such as marine snow, faecal pellets and discarded apendicularian house and that such larvae would not compete for food with those of perciform fishes, which are believed to feed on crustacean zooplankton. Other fish larvae from aggregation families utilize additional types of planktonic organisms for food which may be abundant. Sampey et al. (2007) found that the one surgeonfish larva and nemipterid (sea bream) larvae had eaten appendicularians (larvaceans), while Llopiz and Cowen (2009a) found appendicularians to be important food items of surgeonfish larvae and snapper larvae. Recognition of the importance of these other planktonic groups, such as appendicularians, compared to those traditionally considered primary food items (copepods crustaceans) for larval reef fishes, also complicates the examination of zooplankton density and larval feeding.

7.6 Life in the Pelagic Environment – Late Stages

Once fins and other structures are completely developed, the larva enters its end form, the settlement stage (also known as the "pelagic juvenile"). There may some persistence of "larval" characters (Quere and Leis 2010), but these are eventually lost after settlement. Consistent feeding is probably still important, but fish can survive short periods without feeding, and for some it appears they do not feed during metamorphosis. They develop the capability to potentially move towards preferred settlement environments as swimming ability is sufficient to match or exceed most current regimes encountered and any sensory systems can detect sonic, olfactory and other cues. The fish settle from the pelagic environment into benthic habitats.

The literature concerning the biology of settlement stage coral reef fishes is far larger than that dealing with earlier life history stages. Settlement stage fishes can be captured in a number of manners, identified while alive, used in experiments, and have large otoliths with information on life history recorded in them. Species with spawning aggregations are often among those captured by light traps and nets, and some are quite abundant compared to other species in overall samples. The bluehead wrasse and surgeonfishes are among the most common larvae captured and are resident aggregators with long spawning seasons. Others, typically transient aggregators, such as most of the groupers, are not so common, and make it difficult for

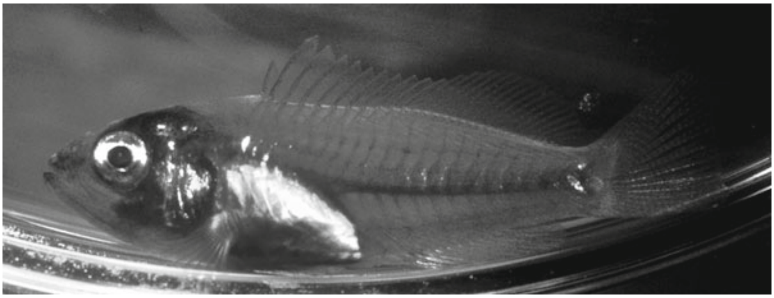

Fig. 7.5 Pelagic juvenile Nassau grouper, *Epinephelus striatus*, photographed after capture in a channel net at Lee Stocking Island, Bahamas. The fish is about 15 mm in standard length and has the transparent body characteristic of fish in the pelagic environment. The gut is covered by silver reflective pigment. Within a few days the fish acquire the pigment typical of juvenile (Photo: Patrick L. Colin)

extensive studies to be done using them that relate directly to the outcomes of aggregations. However, there are a few reports of very large settlement pulses of aggregating species (see Sect. 7.6.3). Some specialized sampling, such as channel nets, can effectively capture some species (Colin et al. 1997; Keener et al. 1988). Crest nets (established on tops of reef using waves and tidal currents to capture fishes) are an alternative method to sample incoming reef fishes, but have not been particularly effective at sampling aggregation spawned fishes with the only family contributing substantially to catches being the surgeonfishes (Dufour and Galzin 1993, Hair et al. 2000).

7.6.1 Settlement and Metamorphosis

The larvae of most species transition into the juvenile stage while still in mid-water and may be able to position themselves in the vicinity of reefs during this stage as many are strong swimmers in both speed and duration (Leis and McCormick 2002; Leis and Carson-Ewart 1997). Stobutzki and Bellwood (1997) found unfed settlement stage individuals of three families (surgeonfishes, snappers, emperors – Lethrinidae) with spawning aggregations to have the highest swimming endurance (time capable of maintaining 13.5 cm s^{-1}) among nine families. If settlement stage fish are fed while swimming, their endurance increases several-fold and some were capable of continuous swimming at 13.5 cm s^{-1}. The settlement stage fishes of many aggregation spawning families tend to be large and capable (Doherty et al. 1994), putting them among those species most likely to be able to move towards settlement habitat. In studies where Nassau grouper pelagic juveniles (Fig. 7.5) were captured while recruiting in channel nets (Shenker et al. 1993; Colin et al. 1997) they were by far the largest and most robust of the many pelagic stages captured (Thorrold et al. 1994), and one of the few species which consistently survived the trauma of net capture and subsequent handling.

Settling fish may “try out” a reef and then quickly return to the water column, not remaining on the first reef they encounter. Once a suitable settlement location is found, the juvenile undergoes metamorphosis, in which it changes its body structure and physiology, losing structures that contribute to survival in the pelagic (transparency, spination), and acquire characters useful in the benthic, environment (pigmention, changes in mouth orientation, changes in alimentary tract for a different diet). Some evidence suggests that fishes stop feeding during metamorphosis, using internal reserves to support themselves for a period of several days.

The settlement behaviour and selection of settlement habitat of some aggregation spawning predatory fishes have been examined (Eggleston 1995; Wright et al. 2005; Nakamura et al. 2009). Quere and Leis (2010) found the Spanish flag snapper, *Lutjanus caponotatus,* to have complex settlement behaviour with strong swimming capabilities and the ability to interact with a variety of reef residents. Leis and Carson-Ewart (1999) reported similar settlement behaviour in the squaretail coralgrouper, *Plectropomus areolatus*.

In the absence of a suitable reef, or any reef at all, how long can pelagic juveniles persist in the plankton? It appears that different species have different tolerances for extension of pelagic life (McCormick 1999b; Leis and McCormick 2002). For some aggregating species they seem to have fairly high limits, if the largest size of pelagic stages is any indication. Among groupers, Smith (1971: 77) reported two transparent “late larvae”, one a Nassau grouper 45.6 mm long and a mutton hamlet, *Epinephelus afer*, 37.5 mm long (whether standard or total length not indicated), taken 8 miles from land in Bermuda and kept in aquaria until they transformed. Randall (1956) noted pelagic surgeonfish larvae (acronurus) as large as 60 mm (average size for settlement about 26 mm SL). Lara et al (2009) provided evidence of delayed metamorphosis in goliath grouper, *E. itajara*, with larval life, based on otolith increments and settlement marks, ranging from a low of around 30 days to as high as 60–72 days. Experimental evidence of delayed metamorphosis is uncommon. However, McCormick (1999a, b) caught settlement-ready convict surgeonfish, *Acanthurus triostegus*, acronuri at night and held them at 3–6 m depth over a 50 m deep bottom inside moored monofilament net cages which delayed their metamorphosis. Control fish, held in benthic cages, metamorphosed within 5 days.

The larval biology of freckled goatfish, *Upeneus tragula*, a widespread IWP goatfish, may be of particular relevance, since it has pelagic eggs. While it has not been observed to aggregate for spawning (some other goatfishes do), it is possible it will be found to aggregate, or that its ELH is similar to aggregating goatfishes. McCormick and Molony (1995) found in an experimental study that larvae of freckled goatfish settled earlier in warmer water with shorter body length and reduced body depth than those reared in cooler water.

7.6.2 Swimming Capabilities and ELH of Reef Fishes

Fisher (2005) indicated that larval reef fishes for several families would be able to “substantially influence their dispersal pattern” through swimming for the last half of their planktonic lives. Four of the families with the highest average swimming speeds have aggregating species (surgeonfishes, rabbitfishes, snappers, emperors). Despite this capability late in larval life, larvae of these same families are weak swimmers early in larval life. For example, Fisher (2005) examined swimming ability in 10 species of reef fishes, but only one, the brown surgeonfish, *Acanthurus nigrofuscus*, had a pelagic egg (also an aggregation spawner). The brown surgeonfish at hatching were the slowest swimmers with a value near zero (Fisher 2005, Fig. 2) reflecting the feeble ability of yolk sac larvae to distribute themselves or control their depth. Overall she found that larval reef fishes (minus brown surgeonfish) increase their swimming speed in an essentially linear relationship with age (for the species examined) and that during the latter half of larval life they swim sufficiently well to be able to influence their location in relation to average currents near reefs. The vast increase in swimming capability with growth needs to be put into the perspective of the entire ELH in that larvae with pelagic eggs will spend roughly the first half of their larval life without the ability to swim against average currents. Once they have the capability to swim robustly, their location in the ocean could be quite far from any shallow water habitat.

7.6.3 Do Aggregation-Spawning Species Recruit as Large Cohorts?

If large numbers of propagules are started simultaneously from a limited number of locations via aggregation spawning, does this produce a corresponding pulse of recruitment by a large settlement-ready cohort at the end of pelagic life? It would seem the prospects for large recruitment pulses from aggregation spawning, particularly from TAs, would be high. For resident aggregators, which often have lengthy spawning seasons, it seems less likely recruitment would be pulsed, unless survival of some cohorts are enhanced by processes during pelagic life. There is some limited evidence to support such a conclusion, but the connections between aggregation spawning and the occurrence of large cohorts is far from certain. Large pulses of recruitment might be produced by non-aggregation spawners which have a short spawning season. Such would probably be indistinguishable from aggregation spawning recruitment pulses. Differential survival in the pelagic stage among fishes which spawn would also tend to produce recruitment in large cohorts. Interestingly, some capture-based aquaculture fisheries are based on catching large pulses of settlement phase larvae (Sect. 8.2.3).

There are records of large recruitment pulses for reef fishes; many from aggregation spawning species or families. Such are known in surgeonfishes, groupers, wrasses, tetraodontiform fishes, bigeyes (Priacanthidae), Moorish idols (Zanclidae) and rabbitfishes (Fig. 7.6). In a large recruitment pulse, high numbers of settlement-ready fishes appear over just a few days and, based on locations where such pulses have been sampled, recruit over reef crests (Dufour and Galzin 1993) in the Indo-Pacific, through tidal channels from offshore waters (Keener et al 1988; Shenker et al. 1993;

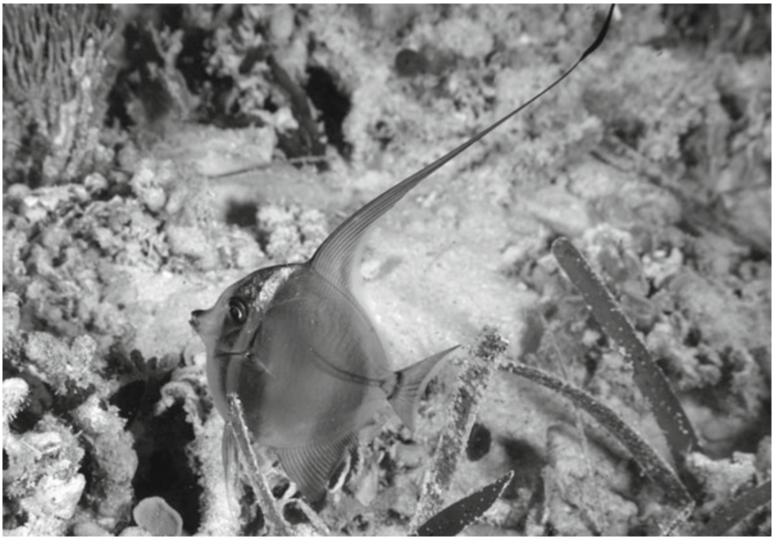

Fig. 7.6 Pelagic juvenile Moorish idol, *Zanclus cornutus*, at the time of recruitment. Photographed at night, the fish has begun to acquire the coloration typical of juvenile fish (copyright Mandy T. Etpison)

Colin et al. 1997) and simply by the appearance of vast numbers of juveniles (Fig. 7.7) where previously there were few or none (Letourneur et al. 1998; Chabanet et al 2005, PLC personal observation).

Instances of massive recruitment by surgeonfishes are well documented from a number of species known to be resident aggregation spawners (Randall 1961, Doherty et al. 2004, Robertson 1983). While not all family members are known to aggregate, it seems likely many others will be added as observations increase. The specialized acronurus larva is useful in that it is easily identified in plankton samples (Oxenford et al. 2008) and is highly adapted for pelagic life. Convict surgeonfish is known to have large fluxes (“regular broad peaks”) of larvae across the reef (Dufour and Galzin 1993, Randall 1961). Planes et al. (1993) reported successive pulses in recruitment of convict surgeonfish in Tahiti, saying they “may reflect reproductive periodicity or result from physical oceanic processes”. Sancho et al. (1997) documented a recruitment pulse of spotted surgeonfish, *Ctenochaetus strigosus*, at Johnston Island. Similar pulses have been observed in Palau on several occasions, most recently in 2009 (Fig. 7.7). They appear as large schools of small individuals on both outer reef slopes and inshore areas, which they would have had to enter through small tidal channels. Such groups are usually subject to very high predation, as often there is not sufficient shelter for fishes (Doherty et al. 2004). The schools formed by the massive recruitment of two species of surgeonfishes in Palau in 2009 (Fig. 7.7) were subject to heavy predation by jacks (Carangidae) and other piscivores. Over a few weeks the size of school decreased and eventually disappeared, the fish presumably either eaten or having successfully taken up residence

Fig. 7.7 School of newly recruited *Ctenochaetus* sp. surgeonfishes in the lagoon inside the western barrier reef of Palau. The fish were present over an open sandy *bottom*. If approached the entire group would swim away from the snorkeler and in general are extremely easily disturbed (copyright Mandy T. Etpison)

elsewhere on the reef. Whether such large recruitment pulses originate from spawning in Palau is not known, but some of the species do aggregate for spawning in Palau. Other species can recruit directly into the reef in vast numbers, and may be subject to predator pressures, but their disappearance is not so easily detected (Fig. 7.8).

There are instances where recruitment occurrence is tied back to reproductive seasons by inference from knowledge of spawning season and recruitment periods. Such may occur for both aggregation and non-aggregating species, although in many cases whether or not aggregation spawning occurs is not known. Spawning by a large population of fish outside of aggregations over a short period of time, given that oceanographic mechanisms may serve to concentrate eggs or larvae, may be indistinguishable from aggregation spawning. Lunar effects may also be hard to see in such cases, although it is possible to back-date otoliths to determine time of spawning.

Pulse recruitment of the Nassau groupers in the Exuma Cays in the Bahamas, directly tied to aggregation spawning, has been documented using channel nets for a period of a few days about 1.5 months after spawning (Shenker et al. 1993; Colin et al. 1997). Additional recruitment may occur in areas other than those fed through tidal channels, but is harder to quantify as such recruitment is not so easily monitored (Colin et al. 1997). Doherty et al. (1994) documented pulse recruitment in the squaretail coralgrouper on the Great Barrier Reef. Doherty and McIllwain (1996)

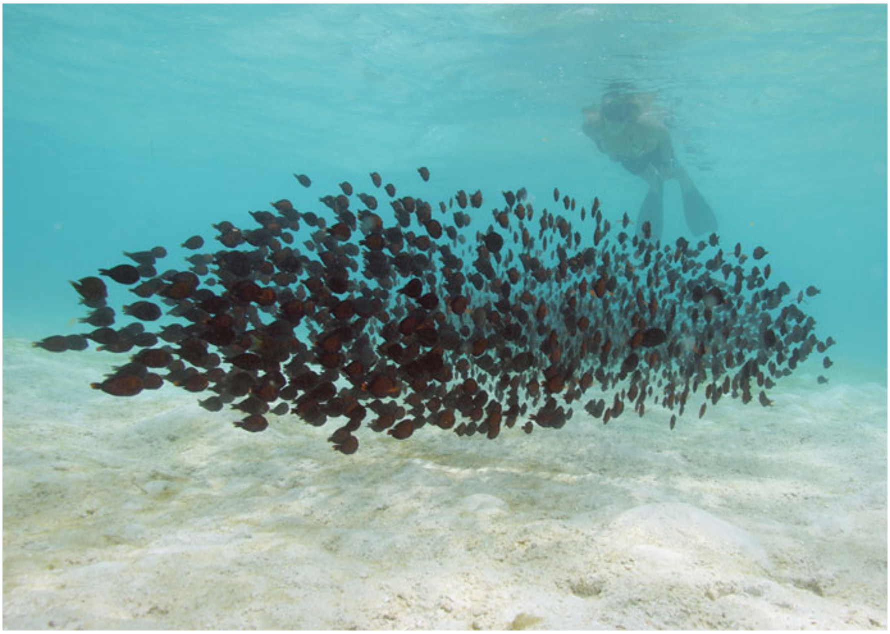

Fig. 7.8 Cloud of newly recruited surgeonfishes, with a few damselfishes in the foreground, on the barrier reef of Palau, April 2009 (copyright Mandy T. Etpison)

found possible pulses of recruitment of some aggregation spawners (snappers) using channel nets at Ningaloo Reef, Western Australia, but for other families where pulses have been seen elsewhere, such as surgeonfishes, few settlement stage larvae were captured.

Relationships between spawning season and recruitment are known in other groupers. Keener et al (1988) showed a clear connection between aggregation spawning of the gag grouper, *Mycteroperca microlepis*, with appearance of juveniles over a few days in nets fished in a tidal inlet. Recruitment of some smaller groupers may not necessarily be a result of aggregation spawning. The coney, *E. fulvus*, spawns in small haremic groups without lunar timing during the winter in the Bahamas and new recruits appear at appropriate times where their otolith increments back-date to known spawning times (PLC unpublished data) so the settlement is seasonal, but does not appear to be pulsed. For other western Atlantic groupers believed to have limited spawning seasons there is a loose relationship between the known months of spawning and the appearance of juveniles 1–2 months later (PLC unpublished data)

The same is possibly true for some small IWP groupers. Dufour et al. (1996) found simultaneously large fluxes of honeycomb grouper, *Epinephelus merra*, for a few days across a number of seaward reef flats in Moorea after the new moon in February and March. Letourneur et al. (1998) and Chabanet et al (2005) reported massive recruitment of honeycomb grouper following storms at Reunion Island, Indian Ocean with up to over 400 individuals per 20 m^2 area and populations falling to near normal levels (only a few percent of those originally seen) within a few weeks, either through predation on or migration of juvenile groupers. While not verified as an aggregation spawner, there is some evidence this grouper may indeed use that reproductive strategy (Chap. 5).

For wrasses large recruitment pulses are known in bluehead wrasse (Masterson et al. 1997) and California sheephead, *Semicossyphus pulcher* (Cowen 1985). Masterson et al. (1997) reported a large synchronous pulse of recruitment of bluehead wrasse to sites on 3 US Virgin Islands in 1 year, but not in 2 other years, while the spawning seasonality of the species varies across its range.

In the tetradontiform fishes (triggerfishes and pufferfishes-Monacanthidae) there are several records of massive and intermittent recruitment, although it is unknown if many species in this group have aggregation spawning. Robertson (1988) reported large-scale recruitment of queen triggerfish, *Balistes vetula*, in Caribbean Panama. Stimson (2005) documented occurrence of large episodic recruitments of the fantail filefish, *Pervagor spilosoma*, to reefs in Hawaii, but its spawning mode is not known. Rabbitfishes are also known to have aggregation spawning and massive recruitments. In Guam, Kami and Ikehara (1978) reported scribbled rabbitfish, *Siganus spinus*, and forktail rabbitfish, *S. argenteus*, juveniles to appear on the reef flats a few days before or after the last quarter moon in April and May. There are reports of "balls" of siganid juveniles occurring in deep reef waters. Aggregation spawning and large recruitment pulses are known for rabbitfish in Palau (Chap. 12.22).

Fishes in some other families, such as Hawaiian bigeye, *Priacanthus meeki*, and Moorish idol, *Zanclus cornutus*, have had bursts of abundance on Hawaiian reefs with subsequent disappearance or dropping back to normal levels (Stimson 2005). It seems likely the Moorish idol may well have aggregation spawning in at least some areas (Palau, PLC personal observation), but nothing is known about bigeye spawning (Chap. 12.19).

7.6.4 Is Mass Spawning of Marine Invertebrates Comparable to Reef Fishes and Does It Provide Any Insight into Reef Fish Pelagic Life?

Many marine invertebrates have a dispersive larval stage, and some spawn at discrete times and places *en masse* (Babcock et al. 1992). While a review of this subject is beyond the scope of this chapter, a few comparisons are useful, particularly when invertebrate spawning has been compared to fish aggregation spawning (see also Chap. 3).

The mass spawning of stony corals (Scleractinia) has been documented from many locations throughout the tropics (Baird et al. 2009), and is often limited in seasonal and lunar periods. Van Woesik (2010), reporting that corals spawn at times of calm wind conditions in different areas, suggested that "spawning during regionally calm periods may also be applicable to other marine organisms, such as fishes" citing Johannes (1981). While this might seem a useful comparison to fish aggregation spawning, the similarities are limited. Many species of stony corals release sperm and egg bundles over a period ranging from a few minutes to as much as an hour relying on eventual mixing and fertilization in the water column. Corals do not, in the sense of reef fishes, aggregation spawn, as they can not migrate to a spawning area, but release gametes over their entire range within a reef area. The sex products are quite buoyant, compared to pelagic fish eggs, and quickly form slicks on the surface that are carried by currents or waves. Wolanski and Hamner (1988) point out that "coral eggs are larger and more buoyant than most other eggs from animals that have a planktonic stage and will tend to float even in areas of downwelling" and that waves disperse larvae across the water's surface. Coral spawn can be thought of more as an oil slick on the surface, than the discrete fertile eggs of fishes which might be distributed in the upper few metres of water (Hamner et al. 2007). Only later (many hours to a few days) do the fertile eggs transform into larvae which leave the surface and swim in the water column for a short larval life, in some only a few days. It might also be relevant that no reef fish is known to synchronize its spawning with that of stony corals.

Some crabs and lobsters are probably the invertebrates whose reproductive and larval lives are most comparable to those of reef fishes. This similarity was also noted by Arvedlund and Kavanagh (2009) who stated "almost all demersal tropical teleost fishes have pelagic larvae that may disperse, in common with most tropical marine decapod larvae". For crabs and lobsters, their already fertilized eggs hatch to swimming larvae, often *en masse*, live in the water column, and have to feed and find settlement habitat at the end of the larval life; all comparable to reef fishes. In Palau, Hamner et al. (2007) found on some days very large numbers of crab larvae among zooplankton normally dominated by planktonic fish eggs largely from aggregation spawning. The mass larval release of terrestrial coconut and Coenobitide hermit crabs are similar to aggregation spawning of reef fishes. As detailed by Fletcher (1993) ovigerous coconut crabs with already fertilized eggs move to shore. "Spawning" takes place after sunset when high tide corresponds with dusk, usually on a semi-lunar pattern with the first and last quarters of the moon. Coconut crabs go through 4–5 larval stages requiring 15–28 days, depending on temperature, and the final larval stage must find a terrestrial environment into which to recruit and emerge from the ocean. Marine crabs are similar, however, although they may release their larvae anywhere in the ocean. The oceanographic mechanisms that might tend to concentrate or enhance survival of fish larvae also affect crab and spiny lobster larvae (Eggleston et al. 1998).

7.7 What Do We Know About ELH for Aggregation Spawning Fishes?

While knowledge of the larval biology of coral reef fishes has advanced significantly in the last decade, much of it concerns species with demersal eggs, such as damselfishes, or small fishes with pelagic eggs (e.g. bluehead wrasse) with little subsistence or commercial value, other than as aquarium trade fishes in some cases. We remain largely ignorant of much of the ELH of those larger reef fishes with aggregations. As Quere and Leis (2010) point out "larger species of importance to commercial and recreational fisheries (e.g. groupers, snappers, grunts-Haemulidae) are particularly poorly represented in studies of larval reef-fish behaviour". There is fragmentary information on a few aggregating species, such as Nassau grouper, but along with concerns regarding human impacts on aggregations themselves, there is a pressing need for studies of these (albeit difficult to work on) species of conservation and fisheries importance which are depleted or near extinction in many areas.

At present, there do not seem to be major differences in or benefits documented for ELH from aggregation versus other spawning strategies. Egg sizes or types, based on the limited data available, do not appear to be correlated with aggregation occurrence. By the time larvae are ready to begin feeding, the densities of reef fish larvae with aggregation spawning are unlikely to be much different from other reef fishes (Chap. 6). Behavioural or physical processes may help to concentrate or disperse larvae, but are not documented for the larvae of aggregating fishes. With the designation of large numbers of marine protected areas in low latitude regions, often with the intention to protect reef fisheries, understanding the larval fish ecology in such regions is becoming increasingly important, but not receiving sufficient attention.

In many respects knowledge of ELH of aggregating species is best known for the early life stages. Many of these fishes are of aquaculture interest, and detailed studies looking at the effect of variables such as temperature, turbulence, light, and salinity, have shown that these can have major effects on survival of a cohort. When the results of culture studies, such as specificity of temperature for survival of Nassau grouper through the yolk sac stage, correspond to the conditions observed in the field during the limited spawning season, this implies that culture work can provide important insight into reasons for recruitment changes or failure. Coleman et al (1999) point out "because spawning and recruitment in aggregating spawners are episodic events, they are subject to the vagaries of environmental conditions, and unfavourable conditions such as low water temperature during planktonic stages can drastically reduce year-class strength".

The existence of critical periods, part of the match/mismatch hypothesis, does seem to occur in ELH. As long as conditions are suitable for life through the yolk sac stage, the initiation of feeding is the first major bottleneck in life history. Once ready to feed the time window to begin feeding is relatively short (Yoseda et al. 2006). Being ready to start feeding at sunset is probably not beneficial to early larvae, which are also unlikely to be able to feed at night, and having to wait 12 h before being able to feed will probably ensure that most larvae will soon starve.

The eggs and yolk sac larvae are 'drifters' initially not active in promoting their retention or dispersal. These are largely determined by where and when they are spawned and it is likely drifters or dye studies could provide reasonable estimates of transport. At the end of the yolk sac stage, swimming ability is limited and directed towards feeding and perhaps making diel vertical migrations in response to light. Passive drifting raises the problem of "wash out", in which larvae would be increasingly dispersed from their natal region and some mechanisms described in Chap. 6 which serve to limit this. Once feeding is successfully initiated, for reef fish larvae in general, under normal conditions starvation may not be an overriding factor in mortality (Llopiz and Cowen 2009a, b). Potentially, predation may have equal or greater importance in larval mortality.

The relative importance of physical versus biological mechanisms of retention will likely change as presettlement fishes develop (Leis and McCormick 2002). Once established in the pelagic environment early stage larvae transition within 2 weeks or less to post-flexion larvae, capable of more extensive swimming and daily vertical movements. Post-flexion larvae may be able to seek out and stay with concentrations of food items, perhaps seeking out convergent fronts with more food items, but also potentially more larval predators. Structures, such as large fin spines in grouper/snapper larvae and spines in acanthurids, may develop that reduce the potential for predation and enhance survival in shallow oceanic waters. Larvae remain nearly transparent, reflective pigment found over the gut area and only those areas necessary to be pigmented, such as the eyes, are easily visible.

While middle and late-stage larval fishes from aggregations are able to swim capably (Stobutzki and Bellwood 1997), there is, as yet, no strong evidence they school (Leis 2006) or utilize the epibenthos during their ELH. Leis (2006) points out “where occupancy of the epibenthic boundary layer has been looked for, it has generally been found, but only in a minority of the species” (e.g. gobiids, sciaenids). For most reef fishes available evidence indicates ELH stages occurring well above the epibenthic. Also, while the possibility of active navigation to settlement habitat through sensory means (hearing, olfaction, wave motion detection, rheotaxis, magnetic sense) has been suggested by numerous authors (Tolimieri et al. 2000; Leis and Carson-Ewart 2003; Simpson et al. 2004; Leis and Lockett 2005; Montgomery et al. 2006; Gerlach et al. 2007; Dixson et al. 2008), there are numerous caveats evident in any application of such information in a broad oceanographic sense. For example, Heenan et al. (2008) commented that all earlier studies on the response of settlement stage larvae using acoustic playback to assess auditory attraction had been done in the same location, often with the single same reef sound recording, and use of a reef sound recording from a different area, did not attract fishes. Most studies have relied on a small suite of families, usually fishes with demersal or orally-brooded eggs, with experiments being carried out either in small flumes or in reef waters on broad continental shelves (Great Barrier Reef lagoon), and are considered applicable only in situations where reefs are from a few 100 of metres to perhaps 1 km away from settlement-stage larvae.

Whether the sensory abilities of settlement stage pelagic larvae are capable of finding reefs from many miles at sea has not been conclusively demonstrated. New efforts, such as the “orientation with no frame of reference” effort (Paris et al. 2008) hold promise of providing detailed information on the behaviour of larvae at sea and how they use their sensory capabilities to locate settlement habitat. Retention mechanisms may help to keep late stage larvae within recruitment range of some reefs, but the occurrence of settlement stage fish far at sea shows the “leaky” nature of the system. For most aggregation spawned fishes “self recruitment” is unlikely, however for some there is a reasonable chance some larvae might recruit into an area that constitutes the catchment for migration to their natal aggregation site. Detailed work on the genetics of aggregation fishes, particularly those with TAs, may illustrate the presence of meta-populations in these fishes.

7.8 Future Work

There is need for more field work documenting spawning output from aggregations, and the short term transport and entrainment of propagules following through to recruitment. There are some outstanding examples of projects that are doing an excellent job of providing at least part of the picture of the importance of aggregations. Work in US Virgin Islands (Beets and Friedlander 1998; Nemeth et al. 2007, 2008) on groupers and snappers has provided a wealth of new information and is perhaps the best example of how protection of aggregations can allow recovery to occur. They have not, as yet, expanded the work to include most of ELH and recruitment. The project in the Cayman Islands looking at Nassau grouper ("The Grouper Moon") project, a relatively small-scale effort with modest funding, is an outstanding example of the type of work that needs to be done, as it has attempted to link aggregation and spawning with the pelagic stage ideally through to benthic recruitment and is being conducted over a multi-year period (Whaylen et al. 2004, 2007). That study takes advantage of an existing, protected aggregation to learn what cannot otherwise be learned, but is applicable elsewhere. Similarly, work on spawning aggregations in Belize, although effort has been variable year to year, has provided much information (Heyman et al. 2005; Starr et al. 2007; Sala et al. 2001) but needs to be continued and make the transition to include studies of the fate of larvae at sea. Research on snappers in areas like Riley's Hump in Florida (Burton et al. 2005) could be expanded in seasonal duration, geographic scope (to more aggregation locations) and continued on into the pelagic stage. Domeier (2004) released drift vials at Riley's Hump at the projected time of spawning to demonstrate the high probability of recruits from that aggregation reaching much of South Florida, yet his effort has not been continued by later researchers documenting aggregation at the site. For so many species, we know bits and pieces about their aggregation and spawning, but the whole picture of their ELH remains unclear. These "whole picture" efforts are needed to include as many locations as possible where aggregations still exist.

Aggregations potentially can be approached from a fisheries oceanography standpoint, by targeting studies during the periods when the largest aggregators are spawning. Methods for doing this are well known from fisheries work in more temperate latitudes and could be applied with some modifications for the tropics. In an area like Palau, while there is a relatively substantial amount known about aggregations, there has been no work done on ichthyoplankton or fisheries oceanography.

While large TAs have a mystique that makes them appealing phenomena to investigate, the smaller and more numerous RA provide many more opportunities to increase understanding of aggregations. RAs occur regularly in many locations and are often easily accessed from field stations. They allow collection of spawning fishes, their gonads and released eggs plus investigations of the relationship between environment and reproduction. RAs are often still found in areas where TAs have largely been eliminated by overfishing. Research methods can often be developed first on RA and then applied to TA at a later time.

The interest of the aquaculture industry in rearing larger reef fish species, many with aggregations, will provide valuable information on those factors important in ELH, as long as those results are published in the open literature. The changes in survival during culture through the yolk sac stage brought about by minor differences in temperature, light, salinity and turbulence (Watanabe et al. 1995, 1996, 1998; Ellis et al. 1997; Sugama et al. 2004; Yoseda et al. 2006) imply those same factors are acting in the ocean and provide a backdrop for assessing environmental conditions when aggregation and spawning occurs. They certainly point to the first week of life being the most sensitive for reef fish with pelagic eggs. A vigorous assessment of the role of temperature regimes in relation to timing of spawning over geographic ranges is needed; there are few data that cover the entire seasonal temperature regime where aggregation spawning occurs.

There is need to expand studies of recruitment by larger, commercially important reef fishes. Light traps are useful for some, but not all, species. Methods such as channel nets, reef crest nets or other passively fishing nets have proven useful. The success of capturing settlement stage Nassau grouper using channel nets in the Bahamas (Shenker et al 1993; Colin et al. 1997) as well as South Carolina (Keener et al. 1988) has not been replicated (attempted) elsewhere. Given the relatively small settlement window known for the species, it would be relatively easy to replicate this effort in other regions with tidal currents during the expected (and other) times of settlement.

The role of maternal nutrition and egg quality (McCormick 1998; Green and McCormick 2005; Green 2008) merits careful attention among aggregating fishes. A benefit derived from aggregation spawning (particularly for transient species) may result from increases in egg quality, through nutritional factors, limited spawning season, and intraspecific behaviour. This could be tested in a number of ways, from comparing nutritional and hormonal status of ovaries of captured fishes, capture of eggs after spawning (Chap. 9), to experimental work. Since egg quality in some reef fishes with demersal eggs can increase ELH survival and growth of larvae, as well as reduce the time in the pelagic phase, this may be of major importance in the evolution and maintenance of aggregation spawning.

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