

PROMOTING MARINE SCIENCE: CONTRIBUTIONS TO CELEBRATE THE 50TH ANNIVERSARY OF *SCIENTIA MARINA*.
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Fisheries oceanography and the ecology of early life histories of fishes: a perspective over fifty years

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SUMMARY: Fisheries oceanography can be defined as the study of the ecology of fishes in the ocean: so defined, it comprises study at all levels of ecological organization—organisms, populations, communities, and ecosystems. The early life history of fishes plays out at each of these levels of organization. A paradigm developed by Johan Hjort at the turn of the twentieth century, along with postulates by Hjort and many of his colleagues that followed, came to guide much of fisheries oceanography through the ensuing hundred years. Research themes that address these postulates can be roughly partitioned as the study of the physiological ecology of the eggs and larvae of fishes in the sea, and the study of the abundance and distribution of fish propagules. Using case studies of organisms and physical processes, considerable progress has been made in understanding the causes of variation in population recruitment, defined either by stage-based models and simulated by individual-based models. Some of this progress has been published in *Scientia Marina*, or its predecessor *Investigación Pesquera*. The causes of variation, however, are interactive and operative at differing, yet often overlapping, spatial and temporal scales. Difficulty in matching spatial scales that typically differ by an order of magnitude or more, will continue to trouble the resolution of causes of population recruitment. Moreover, study of the causes of variation in recruitment has not led to predictive power at an annual scale. Prediction at a decadal scale, using community (or more appropriately larval fish assemblages) and ecosystem level dynamics, is more hopeful.

Keywords: fishery oceanography, fish early life history.

RESUMEN: LA OCEANOGRAFÍA PESQUERA Y LA ECOLOGÍA DE LOS PRIMEROS ESTADIOS DE DESARROLLO DE LOS PECES: UNA PERSPECTIVA DE CINCUENTA AÑOS. — La oceanografía pesquera puede ser definida como la ecología de los peces en el océano: definida de este modo, comprende el estudio a todos los niveles de organización ecológica: organismos, poblaciones, comunidades y ecosistemas. Los primeros estadios de desarrollo de los peces intervienen en cada uno de estos niveles de organización. El paradigma desarrollado por Johan Hjort a principio de siglo veinte, junto con postulados posteriores del propio Hjort y muchos de sus colegas, han servido de guía de la oceanografía pesquera de los siguientes cien años. Los temas de investigación a que conducen estos postulados pueden ser fundamentalmente divididos en el estudio de la ecología fisiológica de los huevos y larvas de peces en el mar y el estudio de la distribución y abundancia de los propágulos. Utilizando el estudio de casos particulares de organismos, se han conseguido considerables progresos en la comprensión de las causas de variación en el reclutamiento de las poblaciones, definido ya sea por los modelos basados en el estadio de desarrollo o en simulaciones basadas en el individuo. Algunos de estos avances han sido publicados en *Scientia Marina*, o en su predecesora *Investigación Pesquera*. No obstante, las causas de variación son interactivas y operativas a escalas espaciales y temporales distintas, o incluso solapadas. La dificultad para ajustar las escalas espaciales que típicamente difieren uno o más órdenes de magnitud, continuarán dificultando la resolución de las causas del reclutamiento de las poblaciones. Además, el estudio de las causas de variación en el reclutamiento no ha alcanzado un poder de predicción a escala anual. La predicción a escala de décadas utilizando las comunidades (o más apropiadamente los agrupamientos de larvas de peces) y la dinámica de los diversos niveles de los ecosistemas, es más esperanzadora.

Palabras clave: oceanografía pesquera, primeros estadios de desarrollo de peces.

INTRODUCTION

As a branch of ecology, fisheries oceanography operates at all of the levels of ecological organization: the organismal (Dayton and Sala, 2001), population (Cushing, 1996), community (Reynolds, 2001), and ecosystem levels (Steele, 1974). At each of these levels, the life histories of fishes plays out (Fuiman and Werner, 2002; Watanabe *et al.*, 1996; and references therein). Early life history stages of fishes (eggs, larvae, and juveniles) must survive, or at least a few must survive, and be recruited to sustain populations through time (Rothschild, 1986; Rothschild, 2000). Populations of fishes compose communities, and ecosystems comprise all other levels of ecological organization (Frank and Leggett, 1994).

The advancement of ecological thought, and fisheries oceanography, in the 20th century can be divided in pre- and post World War II periods. Ecology advanced markedly in the pre-World War II period with the establishment of basic ecological principles (e.g. Golley, 2001). In the post-World War II era, ecology has been preoccupied with attempted synthesis and with a search for unification of these principles. Throughout, fisheries oceanography has dealt with organismal life histories, population ecology, and ecological communities. Though variation in populations of fishes was recognized as a problem at the turn of the last century, the last 50 years have seen a focus on the highly variable nature of population recruitment (Chambers and Trippel, 1997; and references therein) with the hope that an understanding of the factors that contribute to variability could be used as a tool of fisheries management (e.g. Link, 2002). With the realization and renewed appreciation that single populations operate within ecosystems, with the failure of attempts to manage fisheries on the basis of single populations (for maximum sustainable yield, etc.), and with the lack of political will to implement regulation (both national and international (e.g. Bissix and Rees, 2001)), fisheries management has turned attention to the highest level of ecological organization, the ecosystem (e.g. Browman and Stergiou, 2004; and references therein).

Since the founding of *Investigación Pesquera* in 1955, through the transition to *Scientia Marina* in 1988, fisheries oceanography and the early life history of fishes has been a frequent topic of publication. A plea for basic ecological research and for fisheries oceanography (albeit specifically for phytoplankton and primary production, but ramifying

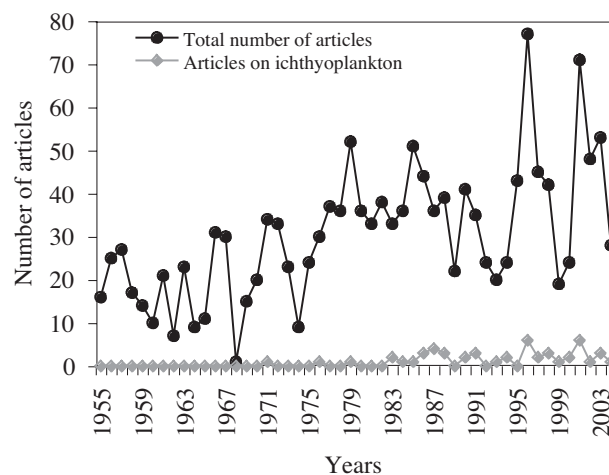


FIG. 1 – Publications on ichthyoplankton in *Scientia Marina* or its predecessor *Investigación Pesquera* versus the total number of papers published by these journals.

into considerations of plant and animal succession, diversity, population abundance, and ecosystem management) was articulated by Ramón Margalef in an essay entitled “The study of pelagic ecosystems” that appeared in the book “Perspectives in ecological theory” (Margalef, 1968). Some of this synthesis was predicated upon detailed work published in the Journal. The publication of articles on fishery oceanography and ichthyoplankton in *Scientia Marina* rose to a high of 14 in 1996 when *Scientia Marina* published a total of 77 articles on all topics of marine science (Fig. 1). Electronic, on-line searches would reveal a similar rise in the number of publications on some aspects of fisheries oceanography and early life histories of fishes in other topical journals over this time period.

This essay offers a perspective on fisheries oceanography and the role played by the early life history stages of fishes in that endeavor. This essay is neither a comprehensive nor exhaustive literature review. The body of literature on this topic is now voluminous. Numerous review articles, theme sections within journals, or supplementary issues of journals (many in *Scientia Marina*), and books chronicle the history of fisheries oceanography and the role of the early life history of fishes in fisheries oceanography. This essay references these reviews, along with papers that are seminal or that mark junctures in thought, or that are more recent or not otherwise referenced. This essay recognizes the population recruitment paradigm broached by Johan Hjort (1914) as the impetus for research and partitions research themes around the postulates that sprang from Hjort’s paradigm. These postulates are

roughly classified as physiological ecology of larval fishes (including feeding success, growth, and predation) and the study of the abundance and distribution of fish eggs and larvae in the ocean as influenced by physical advection. This essay also presents some personal observations of issues and some insights into accomplishments, and offers an outlook for future research.

HJORT'S PARADIGM

At the turn of the twentieth century, Johan Hjort developed a paradigm that attempted to explain the recruitment of young fishes to adult populations (Hjort, 1914); this paradigm set the course for a century of follow-up work. Hjort's recruitment paradigm held that variation of fish populations depended upon varying survival of year classes of fishes through the first year of life (e.g. Chambers and Trippel, 1997; and references therein). Hjort, and his colleagues, followed by attempting to assign variation into two principal causes of mortality of fish larvae: the abundance, or complete lack of, appropriate food, which varies spatially and temporally; and variation in population integrity, which varied through the physical advection of fish propagules to areas favorable, or unfavorable, for development and survival. The first postulate of Hjort's paradigm, success at first feeding, was to drive much of fisheries oceanography through most of the twentieth century (e.g. Lasker, 1981a). The second postulate, that advection disperses or simply transports fish propagules away from, or to, areas favorable for survival, has attracted renewed interest in the post-World War II era, and has been further elaborated more recently as the member/vagrant hypothesis (Sinclair, 1988).

The research directed to Hjort's paradigm has been largely two pronged: (1) laboratory experimental and field study of the physiological ecology, especially trophic ecology, of fish eggs, larvae, and juveniles (e.g. Hunter, 1981; Blaxter, 1988); and (2) study of the abundance and distribution of fish propagules in the ocean (Kendall and Duker, 1998).

PHYSIOLOGICAL ECOLOGY

Physiological ecology is defined as an examination of functional processes that enable an organism to meet environmental challenges. This organismal

level work is essential to establish relationships that are otherwise purely correlative from the observation of animals in the field alone. Observation of the influence of the environment on the physiology of young fishes in the ocean is difficult, and realistic conditions are difficult to simulate in the laboratory, either ship-board or ashore. Because of the artificiality of laboratory environments, experiments must be coupled with observation of physiological response in the sea; hence, physiological ecology. The question of how young fishes function and how they survive in the sea has been an important and sustained thrust of fisheries oceanography (e.g. Geffen *et al.*, 1997; and references therein). In regard to Hjort's paradigm, the research effort has been primarily directed toward feeding and growth of larval fishes, and secondarily to the avoidance of predators.

Feeding success of fish larvae

Issues

Acquisition, digestion, and assimilation of food are physiological processes that are enmeshed within the ecology of any animal. The first postulate to follow Hjort's paradigm, that the lack of suitable food constitutes a major hurdle for first-feeding fishes and consequently their recruitment, still lacks complete and unequivocal empirical proof from the sea. Three principal causes of recruitment failure have been recognized: the match, or mismatch, of larval fish abundance and an abundance of food for larvae; a stable-ocean that effects the match of fish larvae and their food in the vertical dimension; and small scale turbulence that enhances the rate of encounter of fish larvae and their food.

Match or mismatch, first articulated by Cushing (e.g. Shepherd and Cushing, 1990), is predicated on the premise that annual cycles in primary production and subsequent secondary production either match, or does not match, reproductive cycles of fishes, such that the abundance of appropriate (in terms of size as well as nutritional value) food sources coincide temporally with initial feeding of larval fishes. Many case studies have evolved from this original hypothesis (Cushing, 1996; and references therein).

Subsequently, Lasker (1981b) hypothesized that coincidence of appropriate food and first-feeding fish larvae was key to the survival through early life history stages, but that the coincidence was in the spatial, specifically the vertical, dimension. Lasker

hypothesized that it was the coincidence of the chlorophyll maximum layer and first-feeding fish larvae that resulted in survival. When wind forces the destruction of the chlorophyll maximum layer, through vertical mixing, the initial feeding of larvae, and subsequent population recruitment, fails.

In opposition to water column stability and the coincidence of larval fishes and their prey, turbulence, i.e. small-scale vertical mixing of water, might erase spatial segregation of planktonic prey and feeding fish larvae, and increase the probability of encounter. First postulated by Rothschild and Osborn (1996), considerable modeling effort and some empirical investigation in the laboratory and in the sea have followed.

Insight and outlook

In the 1970's there was an apparent disparity between estimates of the ration requirements of larval fishes reared in the laboratory (Houde, 1978) and observations of the concentration of food particles in the sea (e.g. Owen, 1989). This disparity resulted from an over-estimation of the amount of food required for larval fishes, along with the recognition of our inability to accurately detect small-scale concentrations of phyto- and zooplankton appropriate as larval fish food in the sea. The disparity has been partially resolved by the results of physiological energetic experiments (e.g. Kamler, 1992; Wieser, 1995) and the construction of energy budgets for fish larvae that estimate energy requirements and compare these requirements to energy availability (Houde, 1994).

The presence or absence of adequate food and the rate of encounter, are irrelevant to the growth and survival of young fishes unless they can detect, capture, digest, and assimilate this food. This contingency has given rise to intensive laboratory experimentation that attempted to simulate feeding conditions as they exist in the sea. In the 1970's, the speculation was that the larvae of many marine fishes that live in the pelagia were inadequately developed, in terms of their form and function, to be completely successful in the acquisition of energy from a patchily distributed food supply (Fuiman, 1996; Govoni, 2004a). It now appears that while fish larvae are developing organisms, and that development is a continuum until the completion of metamorphosis, the larvae of marine fishes living in the pelagia are capable of performing the requisite physiological func-

tions to the extent necessary to survive, even though they may lack completely developed sensory, locomotive (escape and capture), and digestive systems (Govoni, 2004b).

Match-mismatch is predicated upon primary and secondary production cycles. Translating primary production, through secondary production, to fisheries production has in itself proven problematic (e.g. Nixon, 1988; Houde and Rutherford, 1993; Nielson and Richardson, 1996), in part because of the varying and complex food webs of the pelagia (e.g. Greve and Parsons, 1977; Olsen *et al.*, 2001; Biktashev *et al.*, 2003; but also see Pomeroy, 2001). Moreover, it is apparently new primary production, not primary production *in toto*, that comes into play in the match-mismatch postulate (Richardson, 2002).

Among taxa of fishes, batch spawning (Hunter *et al.*, 1993; and references therein) and bet hedging (e.g. Roff, 1981) largely ameliorate the effects of mismatch. By distributing propagules through time periods that lapse production cycles, fishes can improve the probability of the survival of their larvae.

The match-mismatch of food for larval fishes and first feeding larvae is controlled physically, by temperature as well as wind-driven mixing (e.g. Alcaraz *et al.*, 2002). Temperature, along with photoperiod, controls spawning physiologically, while wind-driven mixing effects the depth of the upper mixed layer, which typically encompasses the euphotic zone, the zone of primary production. The food of larval fishes, largely the proceeds of secondary production, lives within the upper-mixed layer. Partly because temperature, photoperiod, and wind-driven mixing are seasonally variable, and partly because the modes of primary and secondary production lag or are offset temporally in temperate and boreal zones, match-mismatch finds verification largely in the cool-temperate and boreal ocean (e.g. Beaugrand *et al.*, 2003). Match-mismatch is more difficult to assess in the warm-temperate and tropical ocean that lacks this offset.

Starvation in the sea (either because of match-mismatch or simply low food densities) is not well documented at large spatial scales, though patches of larvae in poor condition are evident (e.g. O'Connell, 1980; Amara and Galois, 2001). Many currently unanswered questions arise from this lack of direct evidence at spatial scales large enough to influence population recruitment. Are condition factors thus far proposed for the assessment of nutri-

tional state appropriate measures (Ferron and Leggett, 1994)? Morphometric and histopathological measures can be misleading, inasmuch as skewed morphometric ratios (e.g. Powell *et al.*, 1990; Grønckjaer and Sand, 2003), and histopathological lesions (e.g. Green and McCormick, 1999; Gisbert *et al.*, 2004) can arise by other causes in addition to poor feeding: over eating for example (Mobin *et al.*, 2000)! The use of other indices of condition, including biochemical composition, metabolic enzyme titer (e.g. Browman and Skiftesvik, 2003; and references therein), and RNA/DNA ratios (e.g. Buckley *et al.*, 1999; Clemmensen *et al.*, 1996) has increased in recent years. As an index of protein synthesis, RNA/DNA ratios integrate the varied physiological factors that contribute to growth (e.g. Høie *et al.*, 1999; Fukuda *et al.*, 2001; Gwak and Tanaka, 2002). RNA/DNA ratios, then, measure growth potential (Weber *et al.*, 2003); but on what time scale of response? How synchronous are changes in biochemical composition, enzyme titer, or RNA/DNA ratios with changes in daily ration or the nutritional content of food? The answers are required before these indices can resolve the nutritional condition of larval fishes at operative spatial and temporal scales.

More work that directly links indices of nutritional condition to oceanographic processes and population level variation is clearly warranted. In addition to its direct effect on survival, nutritional condition also influences the buoyancy of larval fishes, which in turn affects vertical distribution (Sclafani *et al.*, 1997). Position in the water column can determine coincidence, or lack of coincidence with food. While condition may be linked to season or to water column stratification (e.g. Bergeron, 2000; Kimura *et al.*, 2000; Catalán *et al.*, 2004), the linkage of condition to population level variation in abundance has proven more difficult (e.g. Pepin, *et al.*, 1999), especially at large spatial scales (Megrey and Hinckley, 2001).

Lasker's postulate of ocean stability was specific for the chlorophyll maximum layer that was, in the study area examined (the California Current Region), populated by naked dinoflagellates. Eating dinoflagellates in substantial and nutritionally significant numbers is restricted largely to the larvae of clupeiform fishes (e.g. Govoni *et al.*, 1983). The larval of other fishes eat dinoflagellates incidentally; dinoflagellates are not their critical first food. While zooplankton, as a whole, is often stratified (e.g. Peterson, 1998), layers of dinoflagellates, compo-

nents of the microplankton, are not of the same spatial scale as layers of zooplankton.

The coincidence in time and space of planktonic food and fish larvae at first feeding, or larval fishes after yolk absorption, depends upon scale, temporal and spatial (Visser and MacKenzie, 1998). In the horizontal dimension, the scales are in the order of weeks, months, and kilometers: in the vertical they are smaller, days, hours, minutes, meters, and centimeters. Too much turbulence erases concentrations of larval fish food, and can diminish encounters between phyto- and zooplankton food, and larval fishes (MacKenzie and Kjørboe, 2000; Fiksen and MacKenzie, 2002; Reiss *et al.*, 2002). The key may lie in the distribution of patches of larvae in time and space (e.g. Dower *et al.*, 1998; Incze *et al.*, 2001).

Recent modeling efforts emphasize the problem of relative scales in resolving the effects of turbulence on larval fish feeding (Galbraith *et al.*, 2004). Turbulence increases net energy gain primarily at low turbulent velocities, $<10 \text{ mm s}^{-1}$, and principally for larval fishes that search for food in spherical or hemispherical volumes. The larvae of most fishes, however, search a wedge shaped volume of water and the affects of turbulence are to be expected at much lower velocities, 5 mm s^{-1} .

Larval fishes frequently have empty guts when collected at sea, irrespective of the time of day when they are collected. Is this the result of stress-induced defecation owing to handling in the net or preservation, or is it an indication of either individual variation in feeding activity within a patch of larvae or an indication of a poor feeding environment? The answer may lie in comparisons of the feeding response of larvae in the sea when prey fields are adequately quantified, and laboratory studies where prey fields are controlled. Examination of the contents of the guts of larval fishes indicates that they are highly selective feeders. Even larvae within the same family that occupy the same parcel of water and that share nearly identical morphology, and sensory and locomotive capabilities, eat significantly different food organisms (Govoni *et al.*, 1986b). Apparent selectivity, however, might simply mean that fish larvae are only able to perceive and capture specific food organisms. Consequently, food of appropriate size, shape, and swimming behavior, not simply food of adequate abundance, is necessary. Resolution of this question is essential for improved accuracy of predictions of the physiological energetic requirements of larval fishes, as well as for considerations of the coincidence of larval fishes and their food.

Fish larvae eat some zooplanktonic organisms that leave little digestive residue in their alimentary canals. As a consequence, alimentary canals appear empty, or are filled with an unrecognizable slurry of chyme. Among the organisms that may account for this unidentifiable chyme are the aloricate protozoans, only recently recognized from laboratory experiments as potentially important constituents of larval fish diets (Hunt von Herbing and Gallager, 2000; Hunt von Herbing *et al.*, 2001). Protozoans in the guts of larvae collected in the sea have been recently identified (Fukami *et al.*, 1999), but a thorough assessment of their importance as dietary constituents awaits further study.

Much of the theory of population recruitment of fishes is predicated upon density dependence, so if larval fishes are capable of diminishing their food supply, they will compound density-dependent mortality owing to inadequate food supply. Gut content load is a required parameter estimate for the calculation of daily rations of larval fishes. It is also the parameter used to develop energy budgets that can be used, in turn, to assess the exploitation of food supplies. Do larval fish impact zooplankton populations? Probably not because estimates of the daily rations of larval fishes indicate that the amount of food required is insufficient to reduce zooplankton populations and there is a difference of an order of magnitude in abundance of larval fishes and of their zooplanktonic food (Dagg and Govoni, 1996; Nielsen and Munk, 1998; Pepin and Penny, 2000). A lingering problem in the determination of daily rations, however, is the correct mathematical form of evacuation rate of larval fishes (Govoni *et al.*, 1986a). The mathematical form of evacuation rate is the subject of argument even for adult fishes (e.g. Jumars, 2000; Andersen, 2001; Bochdansky and Deibel, 2001); it has not been resolved for larval fishes.

Growth of larval fishes

Issues

The growth of larval fishes is central to the estimation of population recruitment (e.g. Beyer, 1989). Growth is a rate process and it is a physiological integrator of all energy spent in osmoregulation and dissipated through friction (heat) in metabolism and locomotion, and energy ingested, digested, and assimilated. As a rate, growth requires the dimension of time. The discovery of a means of the deter-

mining age of larval fishes at an appropriate temporal scale, i.e., days, by counting daily increments on otoliths (e.g. Jones, 1986; Campana, 2001), resulted in an explosion of research and consequent information about growth in early life. The age of larval fishes caught in the ocean and verified by spawning and rearing larval fishes in the laboratory is now obtainable. As a result, the rate of early growth, heretofore assumed to be allometric, is now empirically resolved for a large phylogenetic array of fishes. Further, growth has now been intrinsically scaled with metabolism (e.g. Finn *et al.*, 2002; Osse and Van den Boogaart, 2004).

Insight and outlook

That rapid growth is essential for survival of larval fishes, because it shortens the time that fish larvae spend vulnerable to predators, is subject to debate. Does rapid growth equate to better survival (e.g. Suthers, 1998; Leggett and Deblois, 1994)? Clearly, larval fishes either grow or they die (Anderson, 1988; Sogard, 1997; Nielsen and Munk, 2004). Some inroads into the link between larval fish growth and population variation have been established through the use of the mortality-growth quotient (Houde, 1997), but more work aimed at establishing a link between accelerated growth and population recruitment is warranted. Fishes are highly diverse and they spawn in many different ecosystems worldwide (e.g. Sponaugle and Pinkard, 2004). Categorical statements about rapid growth for all taxa and all ecosystems are subject to skepticism.

Larval fishes collected in the ocean are survivors; presumably small and weak larvae perish through predation (e.g. Heath and Gallego, 1997; Leggett and Deblois, 1994). Larval fishes raised in the laboratory are not subject to predation, unless they are cannibalistic, and some taxa are (e.g. Manica, 2002; Takasuka *et al.*, 2004; and references therein). Yet, runts and brutes simultaneously arise in the laboratory. Growth is a quantitatively inheritable characteristic. As such, variation among individuals may not have simplistic solutions. Moreover, estimates of growth rate determined from fishes collected at sea and those raised in the laboratory are not likely to conform. Coupling these differing growth rates is necessary to fully resolve the connection between growth and mortality (Chambers and Trippel, 1997).

Larval fish change diets as they grow, often before metamorphosis when diets change markedly.

Coupling changes in diet, with accelerations or decelerations in growth rate (e.g. Kaji *et al.*, 1999; Govoni *et al.*, 2003) is another area for fruitful research that will aid in the resolution of growth and mortality.

Predation

Issues

While not explicitly indicated by Hjort and his colleagues as a cause of variation in recruitment, predation on larval fishes is relevant to the food in the sea question; fish larvae must eat to grow and they must grow to better escape predators (Bailey and Houde, 1989). So what eats fish eggs and larvae? Almost everything is a predator; from some other larval fishes, to myriad components of the zooplankton, to filter feeding adult fishes (e.g. Takasuka *et al.*, 2004). Because of their size, shape, and swimming capacities, larval fishes are extremely vulnerable.

Insight and outlook

Sensory perception and locomotor agility that enable predator avoidance, seem adequate defenses for most planktonic predators (Govoni, 2004b). There is no adequate defense for larger predators, i.e., fishes that attack at rapid speed or through suction or filter feeding (e.g. Connell, 2000; and references therein).

The question of what eats larval fishes and, more importantly, how many are eaten remains incompletely resolved. Larval fishes, with little ossified bone, are digested rapidly and leave little residue in the guts of predator. The question of what eats larval fishes might be resolved by immunochemical or molecular-probe approaches to identifying food organisms in the guts of predators. (These techniques should also prove useful in identifying unrecognizable food in the guts of fish larvae, e.g. aloricate protozoans).

So much of the work on predation has been correlative, i.e., correlations between the numbers of predators and prey. Correlations assess the association between or among variables: correlations do not describe functional relationships. Predation, therefore, cannot be appropriately inferred from the presence or absence, or abundance, of predators and prey where there is co-occurrence; predators and prey might simply be segregated in space, com-

pletely, or partially with overlapping distributions. There is a growing body of evidence that links predation to variation in year classes (Paradis and Pepin, 2001; Tsou and Collie, 2001; Munk, 2002), but direct verification, i.e., the establishment of cause and effect, remains necessary.

ABUNDANCE AND DISTRIBUTION OF FISH EGGS AND LARVAE IN THE OCEAN

Describing the abundance and distribution of fish propagules in the ocean is basic fisheries oceanography (Heath, 1992; Kendall and Duker, 1998), and it is essential to the second element of Hjort's paradigm (e.g. Bradbury and Snelgrove, 2001; Dalley *et al.*, 2002; Olivar *et al.*, 2003). Quite simply the advective transport of fish eggs and larvae influences abundance and distribution and provides the mechanism that drives population retention or dispersal of fish eggs and larvae (e.g. Boehlert and Mundy 1994; Hare *et al.*, 2002). Advection also influences the structure of communities, or more properly assemblages (e.g. Smith and Suthers, 1999; Hinrichsen *et al.*, 2003). Many fishes release eggs into the pelagia, typically in the upper 200 m (e.g. Olivar and Sabatés, 1997), where they are more susceptible to collection than are adult fishes that can avoid mid-water trawls or seek protection from bottom trawls in benthic substrates. The consequence is that surveys of planktonic larvae often reveal more diversity in the fish fauna, than do surveys of juveniles and adults (e.g. Shackell and Frank, 2000; Norberg, 2004). Accurately assessing diversity of the pelagia is the key to understanding ecosystem structure and function and is best done with surveys of fish eggs and larvae (Ahlstrom, 1965).

There are always species of larval fishes in the plankton, though total abundance varies seasonally. Fishes spawn in relation to primary and secondary production cycles, and as a consequence, the abundance of ichthyoplankton typically varies seasonally, except, perhaps, in the tropics where production is annually periodic. Larval fishes, by definition, are part of the meroplankton; species are not constant members of plankton communities. As with so many concepts in ecology, community level organization and the definition of an ecological community, have been the subject of debate. By whatever definition, method of statistical identification (e.g. Miller, 2002), or mechanism of control of organization (e.g. Drake, 1991), ichthyoplankton comprises

species assemblages (e.g. Moser and Smith, 1993; Gray and Miskiewicz, 2000; Harris and Cyrus, 2000; Doyle *et al.*, 2002; Munk *et al.*, 2004) that vary in time over short periods according to the frequencies of spawning of adult fishes (e.g. Smith *et al.*, 1999a). In a theoretical sense, multiple populations of larval fishes do not typically constitute an ecological community (but see Acevedo *et al.*, 2002; Munk *et al.*, 2003) that may be in succession toward ecological maturity. Species composition of ichthyoplankton as a whole varies over longer time scales, but this does not owe to ecological succession; it owes, possibly, to ocean climate change (e.g. von Westernhagen *et al.*, 2002).

Documenting the abundance of fish eggs and larvae provides a method of estimating basic population dynamic parameters, including recruitment, that is independent of fishery catch statistics. The most notable of these is the estimation of spawning stock biomass (e.g. Hunter and Lo, 1993; Armstrong *et al.*, 2001). The abundance of older larvae and juveniles is the only fishery independent, empirical estimate of recruitment, though recruitment can be derived retrospectively from daily age determination from otoliths of fishes that survive. With these data, cohorts of larvae can be identified and peaks of cohort abundance possibly linked to year-class success.

Early life histories of fishes have contributed significant advances to population modeling, specifically to models of variation in recruitment, with individually-based models and stage-based models (Chambers and Trippel, 1997).

Insight and outlook

Deriving basic population dynamic parameters from estimates of the kinds and abundance of fish eggs and larvae is fraught with methodological difficulties. For estimates of spawning stock biomass, population fecundity must be known, and this is complicated by the complex reproductive biology of many fishes (batch spawning and hermaphroditism, most notably). Estimates of the absolute abundance of fish eggs and larvae are difficult to obtain, given the patchy distribution of ichthyoplankton, which owes in part to advective aggregation and diffusion, as well as the location of spawning. Sorting of ichthyoplankton collections and the taxonomy of fish eggs and larvae is labor intensive and time consuming. The development of rapid egg samplers (e.g. Checkley *et al.*, 1997), optical and video plank-

ton recorders (e.g. Herman *et al.*, 2004), and acoustic devices, those deployed in the water column (e.g. Peiper *et al.*, 1990; Thomas and Kirsch, 2000; Miyashita, 2003; Meekan *et al.*, 2003; Ressler and Jochens, 2003) and those moored to the bottom (e.g. Flagg *et al.*, 1994; David *et al.*, 1999), might provide partial solutions to these problems, though the technology requires further refinement. (These technological advances, along with satellite-borne remote sensors (e.g. Santos, 2000; Ibelings *et al.*, 2003) will also help solve the problems of the coincidence of larval fishes, their prey, and their predators). Taxonomic verification from net collections by visual examination will, however, always be necessary.

Ecosystem based management of fish populations, was suggested early-on by Walford (1956), yet interest in this approach is now renewed (e.g. Loreau, 2000; Pitcher, 2001; Link, 2002). This renewed interest moves fisheries management away from attention to single populations of single species, to the management of higher levels of ecological organization: communities (or assemblages of larval fishes) and ecosystems (Ulltang, 2003; Beaugrand, 2004). The feature problem with ecosystem management is in definition: how do we define an ecosystem in a pragmatic sense and what parameters are to be measured to provide definition (e.g. Alverson, 2004); where are ecosystem boundaries (Cadenasso *et al.*, 2003)?

Frontal zones can provide physical definition to otherwise apparently homogenous pelagic space and thereby aid in the definition of ecosystems (e.g. Brandt and Wadley, 1981). By definition, fronts are boundaries between water masses (e.g. Olson *et al.*, 1994). Water masses contain communities of zooplankton and assemblages of fish eggs and larvae. Fronts are also where the ecological action is (e.g. the edge effect). They are places where zooplankton, and fish eggs and larvae, can be physically aggregated (e.g. Bjorkstedt *et al.*, 2002).

Eddies can help define pelagic habitats within ecosystems (e.g. Margalef, 2001). Eddies provide the physical mechanisms that might contribute to or deter from population integrity (e.g. Cowen *et al.*, 2000; Paris and Cowen, 2004). Fish propagules can be wafted away from local populations by physical processes within or around eddies, or they can be retained by these same processes, depending upon their vertical position in the water column and the horizontal spatial scale of the eddy (e.g. Hare *et al.*, 1999; Reiss *et al.*, 2000; Allain *et al.*, 2001; Loger-

well and Smith, 2001). The surface of an understanding of the influence of eddies and fronts, and their inherent physical processes, on population recruitment has only recently been scratched.

A century of intensive investigation into singular causes of year-class variation has not yielded appreciable predictive power over annual periods. While variation has pattern, sources, and consequences (Chambers and Trippel, 1997), annual variation is difficult, if not impossible, to predict. The principal recognized causes (feeding success, predation, and advection) are interactive and each has enough inherent variability to make the prediction of recruitment almost hopeless. The key then is to characterize this variability adequately, to accept it as an inherent characteristic of fish populations, and to build models that make predictions over longer periods (Rice, 1999). Longer term (decade) prediction is more hopeful, since it may be linked to ecological regime shifts (e.g. Bax, 1998; Steele, 1998) that are driven by ocean-climate change (Alheit and Hagen, 1997; Hoffman and Powell, 1998; Dambacher *et al.*, 2002; Richardson and Schoeman, 2004). Decade-scale variation, and prediction, requires a broader ecosystem approach (e.g. Miller and Cornuelle, 1999; Pörtner *et al.*, 2001; Bissix and Rees, 2001; Pitcher, 2001; Dambacher *et al.*, 2002; Pedersen *et al.*, 2003; Robinson and Frid, 2003). This approach, and its inclusion of early life histories of fishes, will likely be one of the future directions of fisheries oceanography (Dower *et al.*, 2000).

SUMMARY

Guided in part by Hjort's hypothesis, fisheries oceanography as directed at population recruitment has made progress in understanding the causes of fluctuations of year-classes of fishes, fluctuations that owe to survival or mortality of eggs and larvae. The principal, currently recognized causes of fluctuation are interactive and the operative mechanisms work at differing and overlapping spatial and temporal scales. Difficulty in matching scales that typically differ by orders of magnitude (e.g. Haury *et al.*, 1977) will persist. Much more work toward achieving the appropriate matches in scale remains to be done. Advances in the technology of electronic, *in situ*, sensing devices and in satellite borne remote sensors hold promise. These devices will facilitate and accelerate data collection at synoptic scales.

Present progress in understanding has not led to a gain of predictive power. Prediction over annual scales remains unaccomplished, in part, because data acquisition is costly and labor intensive to the point where the lag in acquisition precludes annual prediction. Again, technological advances in data acquisition should shorten the lag. But, immense annual variation seems to be an inherent characteristic of fish populations.

Gaining predictive power over decadal scales is more hopeful, given an understanding of what drives regime shifts within ecosystems. Predicting or forecasting changes in ecosystems, including regime changes that affect exploitable populations, is a current thrust (Clark *et al.*, 2001), and an endeavor with achievable goals.

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