Wasp-waist populations and marine ecosystem dynamics: Navigating the "*predator pit*" topographies

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Abstract

Many marine ecosystems exhibit a characteristic "wasp-waist" structure, where a single species, or at most several species, of small planktivorous fishes entirely dominate their trophic level. These species have complex life histories that result in radical variability that may propagate to both higher and lower trophic levels of the ecosystem. In addition, these populations have two key attributes: (1) they represent the lowest trophic level that is mobile, so they are capable of relocating their area of operation according to their own internal dynamics; (2) they may prey upon the early life stages of their predators, forming an unstable feedback loop in the trophic system that may, for example, precipitate abrupt regime shifts. Experience with the typical "boom-bust" dynamics of this type of population, and with populations that interact trophically with them, suggests a "predator pit" type of dynamics. This features a refuge from predation when abundance is very low, very destructive predation between an abundance level sufficient to attract interest from predators and an abundance level sufficient to satiate available predators, and, as abundance increases beyond this satiation point, decreasing specific predation mortality and population breakout. A simple formalism is developed to describe these dynamics. Examples of its application include (a) a hypothetical mechanism for progressive geographical habitat expansion at high biomass, (b) an explanation for the out-of-phase alternations of abundances of anchovies and sardines in many regional systems that appear to occur without substantial adverse interactions between the two species groups, and (c) an account of an interaction of environmental processes and fishery exploitation that caused a regime shift. The last is the example of the Baltic Sea, where the cod resource collapsed in concert with establishment of dominance of that ecosystem by the cod's 'wasp-waist'' prey, herring and sprat.
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1. Introduction – *Wasp-waist* ecosystems

Many marine ecosystems of the world share a striking aspect in the configuration of their biological community structures (Rice, 1995). They typically contain a very large number of species at the lower (e.g.,

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planktonic) trophic levels and also a substantial number of species (e.g., predatory fishes, large coelenterates, seabirds, marine mammals, etc.) that, as adults at least, feed at the apex and near-apex levels. However, in many of the more richly productive ecosystems of the world, there is often a crucial intermediate trophic level, occupied by small, plankton-feeding pelagic fishes, that is typically dominated by only one, or at most several, species.

For example, the fish biomass of temperate coastal upwelling systems tends to be dominated by one species of sardine and one species of anchovy. Similarly, temperate ecosystems influenced by western ocean boundary currents may be dominated by a single sardine species (e.g., *Sardinops sagax* in the Kuroshio region near Japan), an anchovy species (e.g., *Engraulis anchoita* in the Falkand/Malvinas Current of eastern South America), or a menhaden species (e.g., *Brevoortia tyrannus* in the Gulf Stream region off the eastern US) Tropical analogs of these temperate ocean ecosystems tend to be dominated by analogous tropical species: sardinellas, anchovellas, thread herrings, etc. Other examples are the herring, sprat, capelin or sandeels of boreal shelf ecosystems. In the Southern Ocean, krill may represent an invertebrate analog. Because of this typical community configuration, featuring many species at the bottom, many at the top, but constricted to a very few dominant species at a mid-level (reminiscent of the body form of a wasp, in which flows of information and material between complex, multi-functional, relatively large thoracic and abdominal body segments must pass through a very narrow tubular waist segment), these ecosystems have been referred to as "wasp-waist" ecosystems (Bakun, 1996, 2005a; Cury et al., 2000, 2004).

Modeling studies have shown that variability in the trophic dynamics of these ecosystems tends to be largely dominated by variations in these mid-trophic level *wasp-waist* populations (Rice, 1995). Typically these populations of small pelagic planktivores vary radically in size, and the variations may have major effects on the trophic levels above, which depend on the *wasp-waist* populations as their major food source, and also on the trophic levels below which are fed upon by the variable, but massive, *wasp-waist* populations. Thus the major control in these ecosystems may be neither "bottom up" nor "top down" but rather "both up and down from the middle" (Rice, 1995; Cury et al., 2000).

The small clupeoid fishes that most often comprise the *wasp-waist* component of an ecosystem, in common with many other marine fish species, have complex life cycles that feature notable "weak links" (Bakun, 1996) that can be disrupted ("broken") by variability in the physical ocean-atmosphere system. This results in wide inter-annual variability in reproductive success.

Moreover, the *wasp-waist* level is generally the lowest trophic level that is mobile, in the sense that it can expand, contract, or relocate its area of operation according to its own internal dynamical and behavioral responses, which may or may not be keyed to environmental changes (Bakun, 2001, 2005b). Prime examples are the well-known range expansions and contractions of the major sardine populations of the Pacific Ocean (Fig. 1). For other prominent examples, see Section 2 in Bakun (2005a), as well as Section 5 (below) of this paper. Such movements in geographical distribution have the potential to massively alter the population productivities and trophic flow structures of the areas involved. Furthermore, these small pelagic fishes tend to have shorter generation cycles than the larger, longer-lived fishes that prey upon them. This gives them a distinctive advantage in that, to the extent that the rapidity of the adaptive processes leading to the changes in geographical distribution may be generation cycle-dependent, they may take advantage of their shorter life cycles to shift their population away from their major predators (Bakun, 2001, 2005b), while their own prey, being planktonic organisms lacking migrational capability, lack the capacity to take offsetting advantage of their even shorter generation times.

A remarkable feature of many regional marine systems is an evident tendency for domination of the *wasp-waist* level of the ecosystem to alternate on multi-annual time scales between two different species groups. For example, there is a widely observed pattern (see Section 7) of alternations in abundance of anchovies and sardines in a wide variety of diverse ocean settings (Schwartzlose et al., 1999; Bakun and Broad, 2003). Moreover, it appears that very abundant planktivorous pelagic juveniles, of fishes that as adults may be semi-demersal or demersal, may at times seize domination of the *wasp-waist* level of a marine ecosystem. For example, in the far northern reaches of the Pacific Ocean, it seems that herring and juvenile pollock might to some degree constitute a species pair more or less analogous to the sardine–
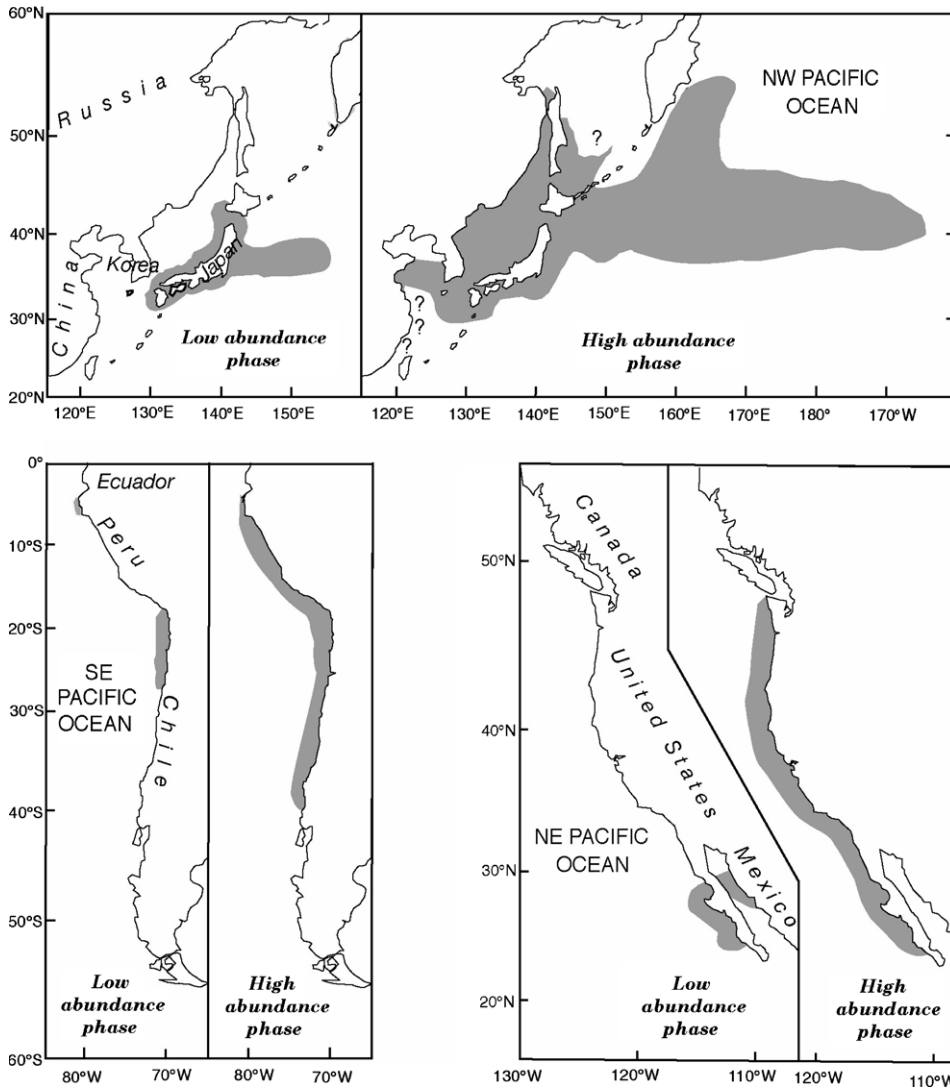
Fig. 1. Changes in distribution corresponding to low and high abundance phases of the three largest populations of Pacific sardines (modified from Bakun, 2005a).

anchovy pair of subtropical upwelling ecosystems, seemingly tending to replace one another in dominating the *wasp waists* of those high-latitude boreal shelf-sea ecosystems. Off tropical western Africa in the 1970s (see Section 2), the *wasp waists* of upwelling ecosystems off Ghana/Côte d'Ivoire and off Senegal appear to have been taken over by juvenile triggerfish. In such situations, the species in such an alternating species pair usually differ substantially in food preferences, migrational tendencies, etc. As a result, one species may drive the population dynamics of trophic levels above and below them in a manner that is distinctly different from that of the alternative species.

Finally, and very importantly, while they are preyed upon by a wide variety of larger fishes, the *wasp-waist* species often prey on the minute early life stages of those same fishes that prey upon them. This introduces an unstable feedback loop into the trophic system whereby a *wasp-waist* species may take advantage of environmental circumstances, or perhaps of overzealous fishery exploitation, to seize control of an ecosystem from its predators and then continue to maintain that dominance over the longer-term, while keeping its predators trapped in a suppressed state (see the example presented in Section 8).

2. Massive outbreaks and abrupt disappearances

In the 1970s, a million tons of snipefish (*Macrorhamphosus scolopax* and *M. gracilis*), which are small (~10 cm adult size) relatives of seahorses and trumpetfishes, appeared off the coast of Morocco (Arístegui et al., 2006), evidently dominating the pelagic *wasp-waist* of that coastal ecosystem for some years. But within a decade the numbers of snipefish (probably about a hundred billion individual adults at their peak of abundance) fell precipitously, and in the following years they have been rarely encountered.

At about the same time but far to the south off the tropical west African coast, a similarly remarkable outbreak was also taking place. In the major El Niño year of 1972, the important *Sardinella aurita* stock in the Gulf of Guinea became exceptionally available to the fishery (Binet et al., 1991), which in that year landed more than twice its previous largest annual catch (Bard and Korentang, 1995). This unprecedented exploitation apparently produced a population collapse which was followed by a remarkable outbreak of grey triggerfish (*Balistes capriscus* = *B. carolinensis*), a deep-bodied fish of a body form normally associated with coral reef systems (Caverivière, 1991). Before the 1970s, this species was rather rare in the eastern Atlantic. But in 1972, sudden increases off Ghana were noted that quickly spread eastward to Togo and Benin and westward to Cote d'Ivoire. In 1981, 500,000 tons of *Balistes* were estimated off Ghana and Côte d'Ivoire. This was 83% of the total estimated pelagic biomass of that area. Several years after the initial outbreak, a new center of outbreak of the species appeared, far to the northwest, off the country of Guinea. By 1982, the biomass in the new zone stretching from Sierra Leone to Guinea-Bissau is estimated to have been as much as 1.3 million tons (Caverivière, 1991). But following a strong rebound in the abundance of *Sardinella aurita* in the 1980s, and its reestablishment as the dominant *wasp-waist* component in the Guinea Current coastal upwelling ecosystem, the abundance of triggerfish dropped precipitously and more recently the species has become rather rare in the coastal upwelling ecosystems of tropical west Africa.

An episode of 'great abundance of file fish' (*Pervagor spilosoma*) in Hawaii in the mid-1980s discussed by Hobson and Chess (1996) appears to have had aspects of similarity to the west African triggerfish episode in that very abundant plankton-feeding pelagic juveniles of a normally demersal population appeared to have taken over and dominated the local pelagic *wasp-waist* over a multi-year period (interestingly, a filefish is a very close phylogenetic relative to a triggerfish).

Sardines and anchovies have undergone similar population explosions or complete collapses in several regions of the world (Schwartzlose et al. , 1999). The famous decline of the California sardine in the 1940s and 1950s and its near total disappearance in the 1960s and early 1970s off the US west coast are well known and documented (e.g., MacCall, 1986). However, since the 1970s, the stock has once again increased in abundance to the point that it is now the basis for a managed fishery. Likewise, on the opposite side of the Pacific, after the Japanese sardine fishery collapsed in the 1930s and 1940s, sardines were unavailable for several decades before suddenly rebuilding their population explosively in the 1970s and early 1980s. After the mid-1980s, they went into another steep decline. Many readers will also be familiar with the gyrations in sardines and anchovy abundance off Peru and Chile in conjunction with El Niño episodes (e.g., Bakun and Broad, 2003; Alheit and Niquen, 2004). Additional examples of similar explosive outbreaks and severe declines of dominant *wasp-waist* populations can be found in Bakun (1996) and Bakun (2005a).

During a period of high abundance of such a population, one assumes that the abundant food source represented may have allowed its predators to increase their own populations somewhat, and certainly to have keyed feeding behaviors toward that dominant prey source. Since the predators on the *wasp-waist* populations are nearly always longer-lived, and so would be expected to vary in abundance less rapidly, one would expect that the relative predation pressure should rapidly intensify during an episode of steep population decline. Indeed, once a steep decline becomes established, it is often not arrested until the population nearly vanishes as a major factor in the regional-scale trophic system. Nevertheless, such radical collapses do not continue to outright extinction, even in the marine pelagic situation where larger predators have hydrodynamical advantages in pursuing and capturing their smaller prey.

3. A refuge at low-abundance

In the ocean, where most organisms are nearly neutrally buoyant, the law of gravity becomes relatively inoperative, and the laws of hydrodynamics take its place (Bakun, 1996). Frictional drag replaces the pull of gravity as the major constraint to active movement. In an environment governed by hydrodynamics, size offers distinct advantages. A larger fish can generally swim faster, while using relatively less energy, than a smaller fish. Furthermore, except in specialized habitats such as reefs, etc., the ocean offers scant cover or safe refuge for prey. In such a setting, because of size-related hydrodynamic advantages, a predator can usually catch a smaller prey, provided it is willing to expend the required energy.

Accordingly, a question arises as to what keeps predator fish populations from simply growing in abundance until they are able hunt the populations of their prey to extinction. Well, one salvation of a prey population must be the sheer mass of water that must be searched or filtered by its predators. The energy expended by a predator in encountering and gathering prey (plus that expended for physiological maintenance, growth, and reproduction) must be matched by the caloric content of the ingested food. Otherwise, it must soon switch its choice of prey, migrate to a location of greater prey density, enter an energy-conserving inactive state to await better feeding conditions, or starve (Bakun, 1996).

But since predatory fish have size-related hydrodynamic advantages that allow them to swim faster and more efficiently than their prey, it is puzzling that they do not simply follow the schools of their prey, continually maintaining contact, and thereby bypass the necessity to search large water volumes or to wait in ambush for long periods in order to locate a meal. One may speculate that the answer here may involve the other necessity of life, oxygen.

The concentration of oxygen even in well-oxygenated seawater is only a few percent of that in air. Thus, acquiring adequate oxygen for metabolic needs presents a distinct problem to marine organisms that do not break the sea surface to breath air directly, but must absorb oxygen in its very dilute dissolved form through membrane surfaces (gills). With increasing body size, surface area increases more slowly than body mass. For example, in simple solid geometric forms the surface area increases as the square (2nd power) of the linear dimension, while volume (and therefore enclosed mass) tends to increase as its cube (3rd power). Thus larger organisms have a smaller surface to volume ratio and therefore have more difficulty in acquiring adequate oxygen to support the metabolic requirements of their body mass than do smaller organisms. This includes fish. As fish grow in size, retaining the same general body form, their gill surface area increases more slowly than their metabolically active body mass (Pauly, 1981). From the standpoint of problems related to oxygen limitation, size is therefore a distinct disadvantage.

Thus, the thing that may prevent a predatory fish from simply staying continually in contact while it exploits a school of its prey is that tracking the continual rapid shifts and turns of the school, and its continual splitting into smaller groups of individuals to later again reform with other perhaps different groups, would put the larger predator into a state of oxygen deprivation more quickly than it would its smaller prey.

Thus the necessity for (1) favorable trophic energy return for energy expended in predatory activity, while (2) dealing with the oxygen disadvantage that a larger predator fish may suffer relative to its smaller prey, may provide a sufficient refuge for prey at very low abundance levels to prevent, under normal conditions, their total extinction by hydrodynamically advantaged predators.

4. The "predator pit"

Based on the material presented in the previous two sections, it seems evident that rather than varying in a density-dependent manner around some equilibrium "carrying capacity", the tendency in *wasp-waist* populations is for occupation of two opposite states: a very low abundance "refuge" state, where there is sufficient relaxation of predation pressures to prevent outright extinction and a state of explosive growth to very high biomass that very often includes major expansions in occupied habitat. Thus the conventional density-dependent fish population dynamics model does not seem to be an ideal conceptual framework with regard to these oceanic *wasp-waist* populations.

Rather, an alternative way to look at these issues appears to have greater explanatory power in these cases. The *predator pit* conceptual framework, where predation probability decreases above and below an interme-
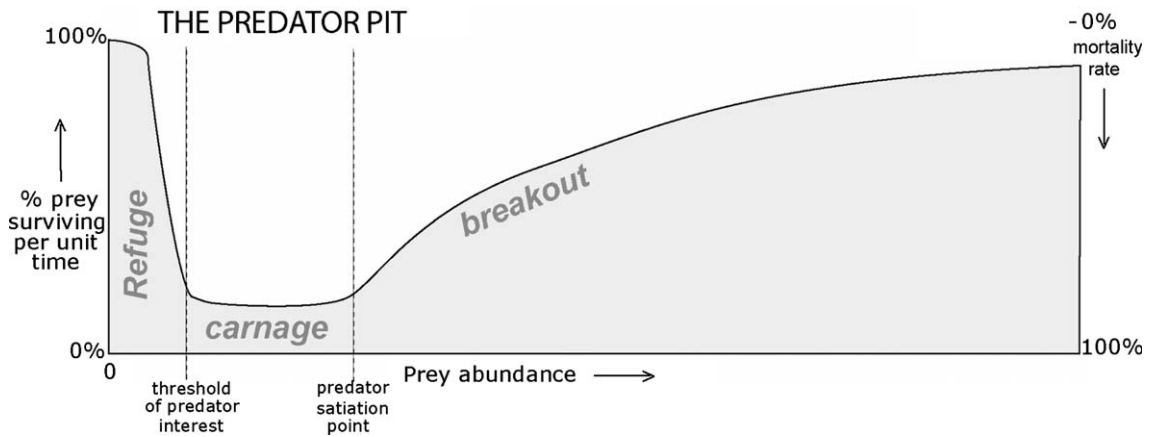
Fig. 2. Diagram of the *predator pit* function. Survival rate (plotted on the left ordinate) increases upwards. Mortality rate (plotted on the right ordinate) increases downwards.

diate level of prey abundance, has been a staple concept in terrestrial ecological modeling for some decades (e.g., Holling, 1965; Gascoigne and Lipcus, 2004). A derivation of a particular *predator pit* formulation, that may be more or less appropriate to small oceanic pelagic fish and similar small prey organisms, as well as to larval or juvenile stages of many larger predatory fishes and other types of marine organisms, is presented in Appendix A. Specifically, below a certain threshold level of prey abundance, predator interest declines steeply to reach a level of zero imposed mortality as prey abundance approaches zero, thus precluding local extinction (the 'Refuge' identified in Fig. 2). However, above that threshold level, each unit of predator abundance actively searches on average a constant, typical volume of water per unit time. Thus, up to a point of satiation, each unit of predator abundance consumes a constant typical fraction of the prey encountered. This results in a rather constant and particularly heavy rate of mortality per unit prey abundance between the "threshold of interest" and the "satiation point" (the "carnage" segment shown in Fig. 3). As prey abundance increases beyond the point of satiation, an individual predator can consume no greater amount of prey per unit time, even as prey density continues to increase. Accordingly, above the "satiation point", as the prey abundance grows, the specific predation mortality rate (fraction of prey consumed per unit time) decreases toward an asymptote of zero, i.e., approaches 100% survival rate as abundance approaches infinity (the "breakout" segment indicated in Fig. 2). Note that according to this formulation (presented in detail in Appendix A), the
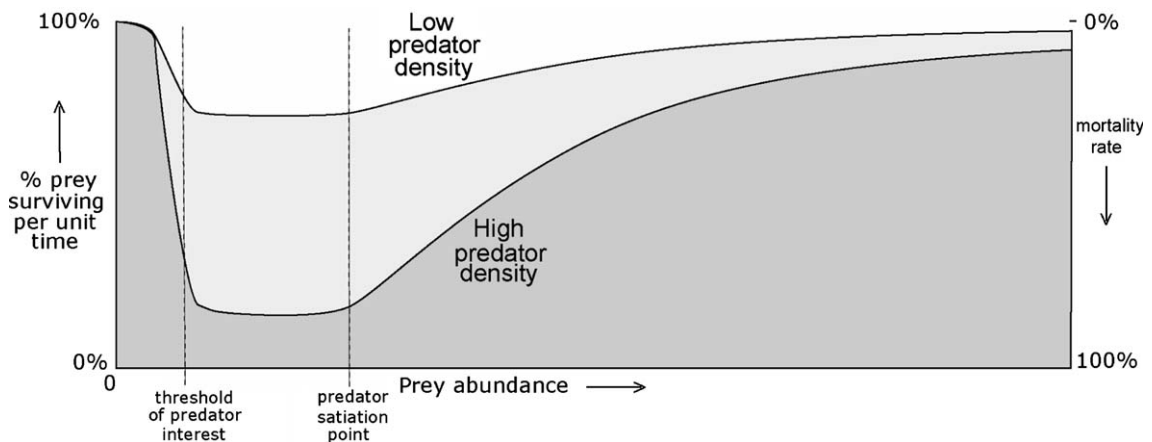

Fig. 3. Diagram illustrating the change in "depth", but constancy in shape, of the *predator pit* function at different predator densities (i.e., abundances).
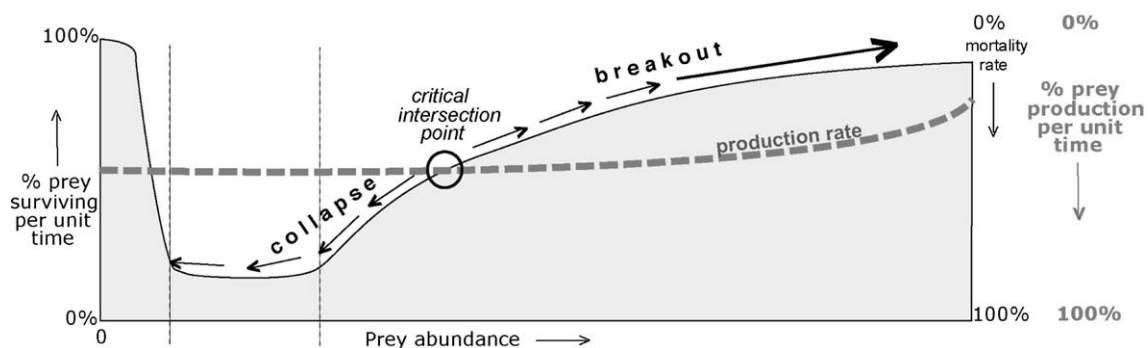
Fig. 4. Production rate curve (biomass produced per unit biomass per unit time – dashed grey curve) of the prey population superimposed on its *predator pit* function. A critical intersection point (circled), where the two curves intersect, marks the abundance level above which the rate of production exceeds the rate of predation mortality and the population increases (prey population "achieves breakout") and below which the rate of predation mortality exceeds the rate of production (prey population "collapses into the pit").

basic form of the *predator pit*, being firmly anchored at its deepest extent to the "interest" and "satiation" abundance thresholds, does not change with predator density but merely deepens or shoals with increases or decreases in predator abundance (Fig. 3).

Now superimpose a curve (the thick dashed grey curve in Fig. 4) denoting the specific production rate of the prey population (plotted positively downward; see scale at right of diagram) onto the basic *predator pit* template introduced in Fig. 2. (Here, the slight curvature of the grey dashed line is intended to suggest the possibility of density dependence in the production rate.) The intersection (indicated by the circle around it) of this curve with the *predator pit* curve marks the abundance level above which the prey population will grow ("breakout") in an accelerating manner and below which the population will decrease ("collapse into the pit") in a similar accelerating manner and then continue to decrease until its abundance level finally reaches the extremely low-abundance "refuge".

Note that should density-dependence in the production rate be strong enough, there would be two intersection points of the two curves and, in a "steady-state", a resulting point of population stability at high biomass (such as would occur in Fig. 4 somewhat beyond the right limit of the diagram as drawn). However, in viewing the historical dynamical behaviors of these populations, it appears that such "steady-state" dynamics may be unusual. For one thing, the tendency to expand the habitat occupied as population increases (addressed in the following section of this paper) would act to dilute increases in density-dependent effects. Rather, in real marine ecosystems, the situation is probably nearly always a highly transient (i.e., non-"steady-state") one, in which the response of predators to a growing food source would act to continually deepen its *predator pit* as time proceeded. As the *predator pit* deepened, the critical intersection (circled in Fig. 4) would progressively move to the right of the diagram, thereby eventually (perhaps abetted by some environmental variation that may temporarily reduce local abundance) intercepting the current population abundance level such that the prey population falls back into the "pit" and toward its low-abundance "refuge" level before it ever actually approached any stability point established by density-dependent control mechanisms.

5. Habitat expansions

The pattern of radical habitat expansions (Fig. 1) coinciding with outbreaks in abundance of Pacific sardine populations has been introduced in Section 1 of this paper. Likewise the progressive geographical expansion of the West African triggerfish outbreak in the 1970s has been discussed in Section 2. Several other similar instances are outlined in Section 2 of Bakun (2005a). In addition, during its rebuilding phase in the late 1970s and early 1890s, the *Sardinella aurita* population in the Gulf of Guinea appeared to shift westward from its traditional center off the country of Ghana to extend its abundance along the coast of the neighboring country of Côte d'Ivoire (Binet, 1995). As of this writing, current reports (Carl van der Lingen, pers. comm.) suggest that the South African sardine may be expanding its habitat eastward as the population rises, with the

centroid of spawning distribution shifting eastward across the Agulhas Bank and the range of the population shifting from its earlier base in the Atlantic toward the Indian Ocean side of the southern end of the African continent.

Does the increase in abundance induce the habitat expansion, or does habitat expansion provide the basis for increase in abundance? The answer, as is probably the case in most such artificially dichotomized "the chicken or the egg?" discussions concerning marine ecosystems, is likely "both" – with both sides of the issue developing simultaneously with continual positively reinforcing feedbacks operating between them.

The *predator pit* concept may offer some insights into the mechanism that accounts for these feedbacks. Suppose that during a low-biomass period, the population in one small sub-area were to somehow, e.g., as a result of stochastically encountering some fortuitous environmental "loophole" (Bakun and Broad, 2003), manage to grow sufficient abundance (i.e., to "leap over" its *predator pit*) to reach the intersection point (circled in Fig. 4), and to thereby "break out" of the *predator pit* trap. It could then pass to a phase of non-linear acceleration in its population growth (i.e., as the difference between its net rate of production and its net rate of loss to predation continually increased) wherein its abundance level would move rapidly toward the right of the diagram. This would soon produce a local excess in population which could then export members to an adjacent sub-area, thereby helping to "fill up the pit" in the new area with sufficient newly imported prey to satiate the existing predators and thereby initiate a similar "breakout", even in a situation where the local population component could not possibly, by itself, grow through "carnage" zone of that particular sub-area's *predator pit* so as to achieve such a "breakout" on its own. This process might then progress in a sub-area by sub-area "domino effect", with the population growing and the area it occupies steadily expanding in concert.

Of course, the process that may guide the geographical directionality of the exports of population from one sub-area to another is a different, perhaps more complex issue. It could be mere diffusion (i.e., "random walk", etc.) from one environmentally suitable zone to another, perhaps mediated behaviorally by some perception of "comfort in numbers". Or it could be a more directly adaptive process, possibly independent of any environmental cues whatever, driven by a dynamic mechanism such as "school-mix feedback" (Bakun, 2001, 2005b).

6. Larval "predator pits"

Fish larvae generally represent only a very small fraction of the total number of similarly sized potential prey organisms (e.g., copepods, etc.) present in a volume of seawater. As a result, when the abundance of larvae of a given fish stock falls to very low values, this may not serve to cause interruption in specific predation mortality, as the predators may continue feeding on alternate prey items of similar size while continuing to capture any fish larvae encountered, (perhaps even preferring a naked fish larvae that it may happen to come across to horny, spiny crustacean alternatives). Thus the "refuge" at the low abundance side of their relevant predator pit may be absent for larval stages of fish species.

Rather, such refuge from predation might occur only when the total composite density of all similarly sized zooplanktonic prey items falls to very low values. This may be the reason that many marine fish species seem to choose very oligotrophic ocean areas as spawning and nursery sites (Bakun and Broad, 2003). For example, the North Pacific albacore tuna (*Thunnus alalunga*) are caught as juveniles in surface fisheries in the richly productive temperate-zone ecosystems both of the Kuroshio–Oyashi confluence of the western North Pacific and the California Current upwelling system of the eastern North Pacific. Adults are caught in longline fisheries over very large areas of the tropical and temperate North Pacific. However, rather than spawning in food-rich regions, the albacore travel immense distances to spawn in the tropical zone of the west-central North Pacific, which is a region of quite low average primary productivity (FAO, 1972). Likewise, the Mediterranean Sea, the most important spawning grounds for North Atlantic bluefin tuna (*Thunnus thynnus*) is known to be a quite oligotrophic sea. Some significant upwelling regions do exist within the Mediterranean, but the bluefin do not appear to seek out those as sites for reproduction. Rather they seem to prefer locations characterized by particularly low primary production (such as the area near the Balearic Islands, etc.). Moreover, surveys of tuna larvae made under the Spanish TUNIBAL Project have indicated that even around the Balearic Islands, the larvae are not necessarily found in the plumes of somewhat richer water identified in satellite ocean color imagery, but rather seem more often to be found in the areas of clearest water situated between the richer

plume zones (Garcia et al., 2001). This is in spite of the fact that tuna are known to have extremely voraciously feeding early life stages (Hunter, 1981).

Sardines, a very different type of fish, exhibit a somewhat similar response. Sardines are species obviously adapted to highly productive ocean conditions (upwelling areas, etc.), but they seem often to experience better reproductive success, at least in the eastern Pacific, during anomalous seasonal warm events, El Nino episodes, etc., which are known to be characterized by abruptly lowered primary productivity (Bakun and Broad, 2003). They also have markedly increased their population sizes during the El Niño-dominated period from the early 1970s to mid-1980s. And a very recent empirical study (Agostini et al., in press) has directly linked improved local sardine reproductive success to decreased values of what may be the best available multi-decadal index of zooplankton density that exists for any ocean area, the CalCOFI zooplankton volume data set (Smith, 1971).

7. Sardine–anchovy alternations

In contrast, the opposite member of the sardine–anchovy alternating pair, the anchovy, reproduces most successfully in highly productive cool inter-annual events such as La Niña episodes. This may offer a clue to the mechanism behind the seemingly paradoxical situation in which these two *wasp-waist* species alternate in abundance, in a wide variety of very diverse ocean settings (Bakun and Broad, 2003), when substantial direct interactions (preferential predation on the other's eggs and larvae, competition for limiting resources, etc.) appear to be lacking.

In the ocean, for planktonic organisms such as a fish larva, "food heaven" almost invariably equates to "predation hell". In such zones, which often occur where *enrichment*, *concentration*, and *retention* mechanisms combine in the proper sequences to form *ocean triads* (Bakun, 1996), growth may be very rapid. And it had better be rapid, because in such circumstances death typically arrives very quickly (i.e., a deep *larval predator pit* is generally the price to be paid for access to a high rate of larval growth). In such circumstances, growing furiously through the various size-dependent predation fields can be a prerequisite to survival.

Bakun and Broad (2003) rationalized the pattern of out-of-phase abundance swings between sardines and anchovies as being the consequence of the different ways in which the two species manage to strike a favorable balance between the growth and predation factors. Here that argument will be elaborated based on the *predator pit* formalism.

First, it is useful to review the special capabilities and characteristics of each of the two types of species. Sardines are particularly adapted for migration. In the case of sardines of the genus *Sardinops* in particular, there may not be another fish of its size that may regularly migrate such long distances. For example, it is believed that before the major population collapse of the California sardine that occurred near the middle of the past century, adults migrated annually from the spawning grounds in the southern California Bight, all they way to Canadian waters near Vancouver Island, a distance of nearly 2000 km (Parrish et al., 1981).

Moreover, sardines feature particularly fine-meshed filtering apparatus in their gillrakers (Van der Lingen, 1994). They are able to filter much smaller particles than can anchovies. Consequently they are able to derive some degree of sustenance from the very tiny particles that may characterize some of the oceanic areas through which they must migrate even in good conditions and that may predominate throughout their range of distribution during El Niño conditions.

Moreover, sardines are serial batch spawners (as are anchovies, sprats, tunas, etc.). They spawn every several days during extended spawning seasons. Thus sardines employ the combination of their migrating capabilities, their ability to feed on very small particles, and their serial spawning habits, to range about the ocean, feeding and spawning, thereby automatically testing for a favorable reproductive "loophole" (Bakun and Broad, 2003) in the fields of predation on their eggs and larvae.

On the other hand, anchovies are not efficient migrators and tend not to use migration extensively in their life strategies (an exception being the South African anchovy population that operates within the special configuration of the Southern Benguela marine ecosystem). The "stay at home" tendencies of anchovies result in minimal migrational energy expenditures compared to those of sardines. Moreover, anchovies do not require size-related hydrodynamic advantages to the degree that the more migratory sardines do and consequently have less need to grow as large. Consequently, they can have shorter life cycles and become highly fecund earlier in life. In addition, because of the much coarser filters in their gillrakers, anchovies can efficiently "push" a

much larger "filter basket" and so are particularly efficient in gathering the large nutritious food particles which are abundant in "good times". As a result, anchovies can use these sources of relative efficiency to allocate relatively more trophic energy to growing rapidly and in producing copious amounts of reproductive product.

During cool seasonal events (La Niña episodes, etc.), in the eastern Pacific, primary productivity is high and zooplankton are abundant. This abundance includes predatory zooplankton (medusas, ctenophores, euphasiids, arrow worms, predatory copepods, etc.) that prey on fish larvae as well as on other zooplankters. Moreover, the rich zooplankton concentrations may attract large numbers of nektonic zooplanktivores (scombroid fishes such as mackerels and horse mackerels, squids, etc.). And what is more, the batch-spawning scombroids may in the process spawn their own voraciously predatory larvae, for which the less active, slower growing anchovy or sardine larvae may be easy prey.

Thus during such cool, highly productive events, the sardine/anchovy *larval predator pit* is deep, which moves the critical intersection point (circled in Fig. 5a) to the right of the diagram. In such a case, the sardine production rate may not be high enough to avoid their current abundance level being intercepted by the rightward-moving intersection point. If this happens the sardine population may "fall into the pit", and collapse to a low abundance level. On the other hand, under these particularly good growth conditions, the relative efficiencies of the anchovies (very large coarse-meshed "filter baskets", ideal for gathering the large, nutritious food particles that are abundant under these conditions, the energy savings associated with non-migratory life style, early age maturity, etc.) may yield such high production and growth rates as to completely circumvent even the very deep *predator pit* that typifies such conditions (as the anchovy growth curve illustrated in Fig. 5a "slips under" the *predator pit* curve entirely), allowing a breakout in anchovy abundance.

In contrast, during a warm episode (e.g., El Niño, etc.), when the ecosystem as a whole becomes much less productive, the *larval predator pit* tends to become much shallower (Fig. 5b). Both the sardines' and the anchovies' growth and production rates would diminish in the much more poorly productive conditions. But, since the sardine has filters adapted to the very small particles that are available in such conditions, and migrates widely in search of more favorable "pockets" where better food conditions might happen to coincide with the reduced predation that occurs (even on adults) under that situation, the sardine production rate may fall only slightly, such that its production rate curve can circumvent (fail to intersect) the *predator pit* curve, enabling sardine abundance to increase explosively (Fig. 5c). At the same time, under such poorly productive conditions, the water column may contain relatively few food particles large enough to be retained on the anchovies' coarse gillraker filters. As a result, the anchovy production rate may collapse so precipitously (i.e., nearly to zero) that the production rate curve may intersect even the shallow *predator pit* curve, causing the anchovy to collapse into the "pit" in this case (Fig. 5c).

Thus out-of-phase abundance alternations between anchovies and sardines may occur entirely without adverse interactions (competition for resources, preferential predation of one species on the eggs and larvae of the other species, etc.) between the two species, but merely as a result of inter-year variations in the background primary productivity of the ecosystem. Anchovy collapse may occur in poorly productive conditions due to that species' inability to produce enough offspring to take advantage of a correspondingly shallow *predator pit* and of the associated reduced need for rapid growth, whereas sardines may collapse in richly productive conditions due to an inability to benefit sufficiently from those conditions to produce large enough numbers offspring, even though these offspring may be able to grow very rapidly, to overcome the very high mortality rates associated with the very deep *predator pit* that such conditions may typically generate.

8. Cod and sprat in the Baltic Sea

The recent history of fisheries in the Baltic Sea, where in the past several decades the cod stock has collapsed and not rebounded, provides an example of the potentially unstable feedback loop (pointed out in Section 1 of this paper) that results when *wasp-waist* species prey on early life stages of their dominant predators.

The Baltic Sea is one of the largest brackish water bodies in the world. It is connected to the Atlantic Ocean by two very narrow and very shallow (<20 m) passages. A low-density surface water layer generally overflows to the Atlantic over the shallow entrance sills; a strong halocline overlies higher density, more saline waters near the sea bottom. The brackish conditions result in a very simplified fish fauna such that only three species,
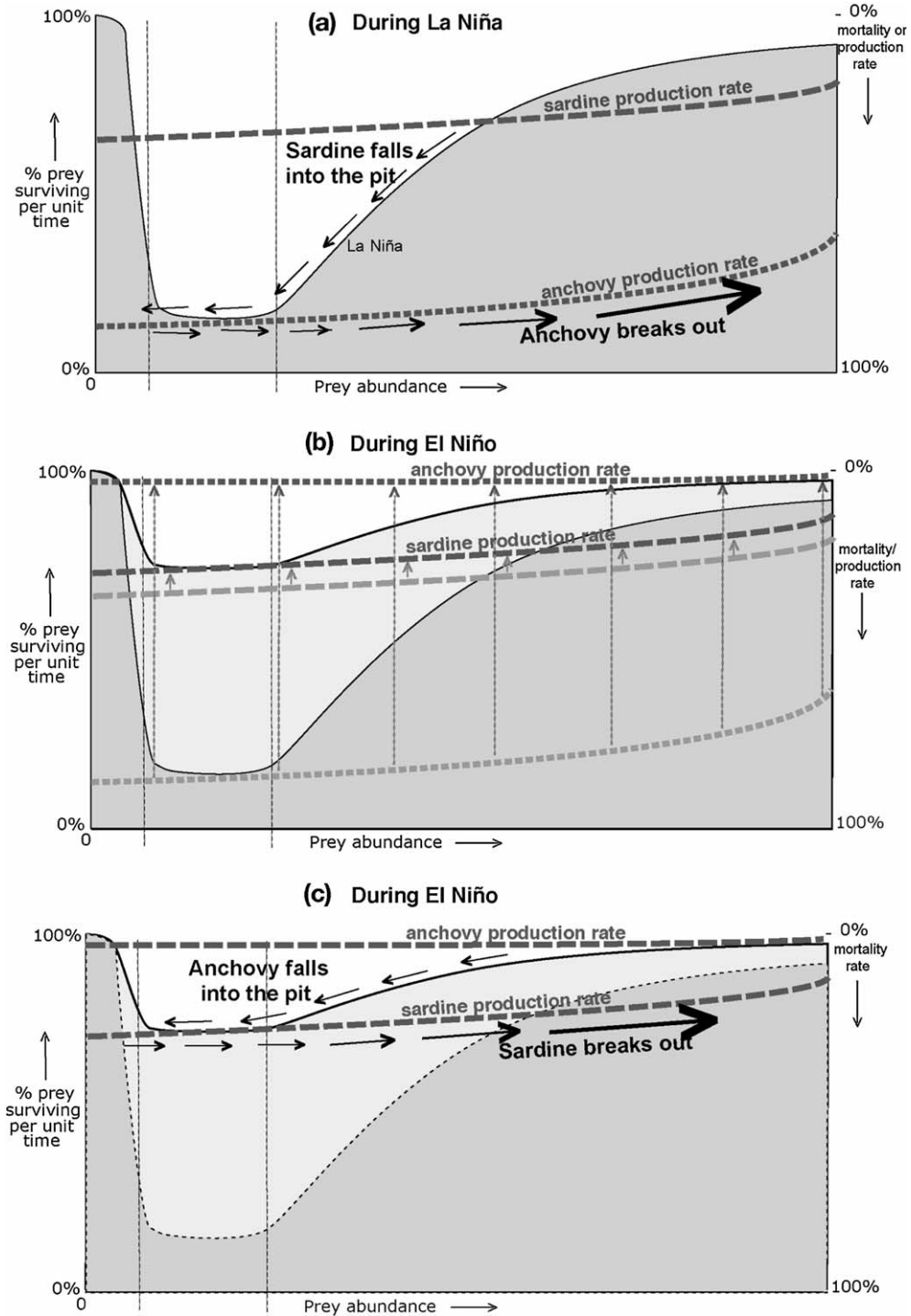
Fig. 5. Warm event (El Niño) – cool event (La Niña) contrast in eastern Pacific boundary ecosystems. (a) During a "cool" episode, system productivity is high and the *larval predator pit* is deep; the high production rate of anchovy in such a situation (see text) may allow a breakout of anchovy abundance even while the sardine population collapses because of inability to raise its production rate enough to counteract the heavy predation and keep its abundance level to the right of the critical intersection point (circled). (b) During a "warm", less productive, episode, the production rates of both sardine and anchovy may decline, but much more drastically in the case of anchovy. (c) As a result, anchovy may experience population collapse, while sardine may achieve a "breakout".

cod, herring and sprat, constitute some 95% of the fishery landings (Sparlholt, 1994). Cod is the major predator in the system. Its most important prey are the *wasp-waist* species, herring and sprat, both of which are clupeid plankton feeders. The unstable feedback loop results from the fact that herring and sprat have been identified as major predators on cod eggs in the Baltic (Köster and Möllmann, 2000; Jarre-Teichmann et al.,
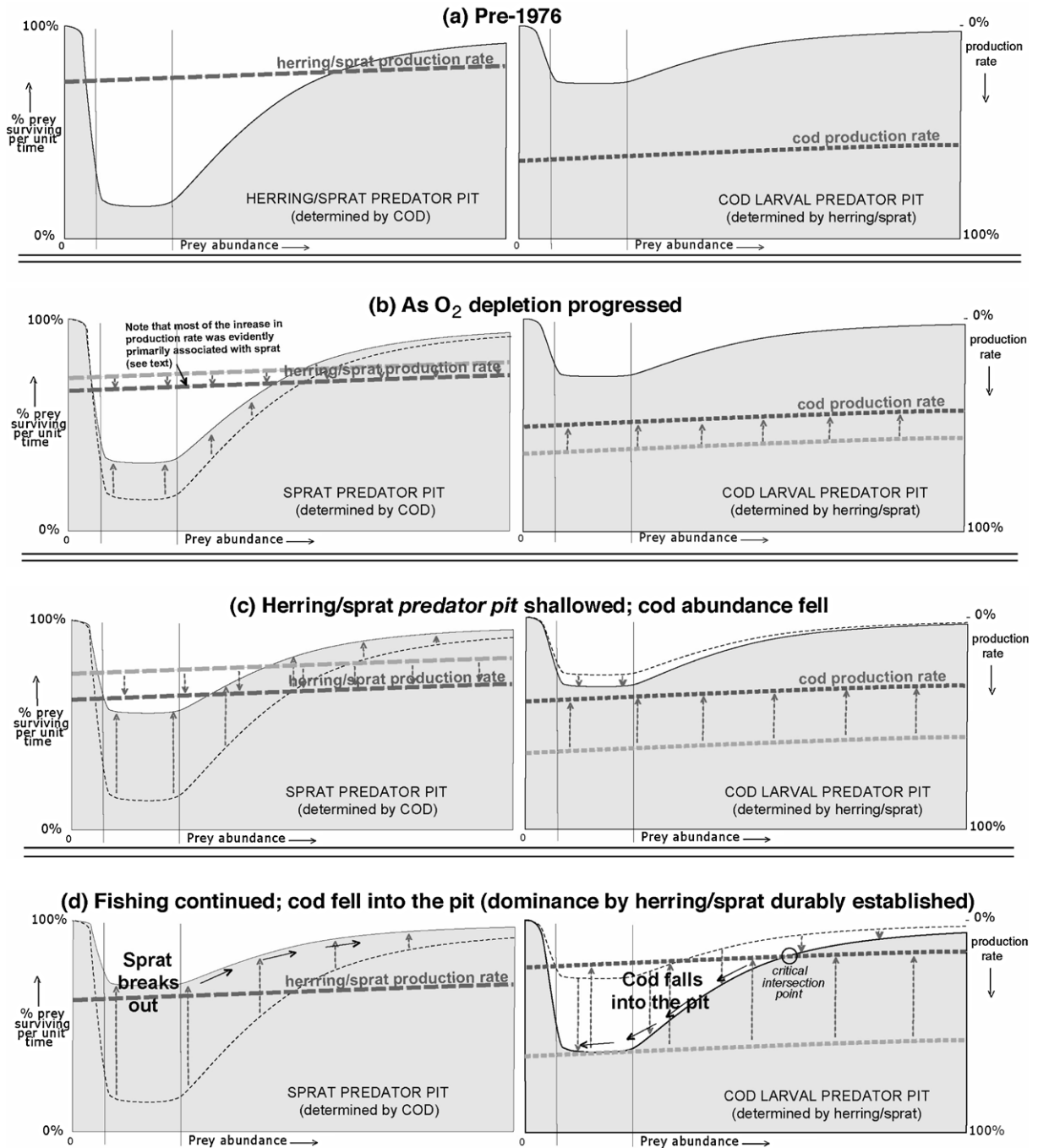

Fig. 6. Temporal progression in the Baltic Sea as dissolved oxygen levels at depth declined during a period of extended lack of bottom water renewal after 1976. (Even after renewal in 1993 brought deep oxygen levels back to pre-1976 situation, the cod resource was unable to rebuild itself – evidently due to predation on its eggs and larvae by the *wasp-waist* populations of sprat and, to a lesser extent, of herring).

2002). The cod eggs occur in densest aggregations within or just below the halocline, which is precisely the zone where the clupeids tend to concentrate feeding activities during their main daytime feeding period (Köster and Schnack, 1994).

The stagnant waters in the deeper basins are renewed only at quite long intervals, between which the oxygen concentration in the deeper zone becomes progressively lowered. A major renewal event took place in 1975/76. This was followed by an unusually long 16-year period of stagnation of the central Baltic deep water (Matthäus and Lass, 1995). Cod eggs have a density such that in most of the ocean areas in which cod occur, their eggs are neutrally buoyant in the upper 20–50 m. In the Baltic however, the lowered salinity causes the eggs to reach neutral buoyancy much deeper in the water column, where they may be exposed to the lowered oxygen conditions in the stagnant near-bottom waters. Cod eggs will not develop, or hatch successfully, at very low oxygen levels (MacKenzie et al., 2000). Throughout the 1980s, as oxygen availability in the deep layers declined, cod have been subject to declining reproductive success (Köster and Möllmann, 2000; Köster et al., 2003a).

Meanwhile, in the decade from the mid-1980s to the mid-1990s, the sprat population increased dramatically (as much as 800% according to the estimates of Köster et al., 2003a). In addition to the relaxation of predation pressure due to the cod decline, environmental factors may also have been involved in this increase. For example, Köster et al. (2003a) infer that warm winters since the 1980s may have favored sprat egg production and egg survival, as well as larval growth and survival. Moreover, potential changes in the mesozooplankton community may have produced better sprat larval food than cod larval food (Grauman and Yula, 1989; Kalejs and Ojaveer, 1989; Köster et al., 2003b).

This chain of circumstances can be simply visualized according to the "predator pit" conceptual framework. Prior to the extended period of bottom water sagnation, herring and sprat abundance appear to have been controlled by predation mortality imposed by the cod (Fig. 6a, left panel). At the same time, predation on these *wasp-waist* species would have kept the cod's egg/larval predator pit shallow (Fig. 6a, right panel). But the waning of cod abundance through the 1980s would have progressively shallowed the *predator pit* for herring and sprat, at the same time the production rate of sprat may have increased due, as mentioned above, to warmer temperature conditions and perhaps to better larval food availability (Fig. 6b and c, left panels). Whatever the case, the sprat population grew dramatically in abundance which would have progressively deepened the egg/larval predator pit of the cod (right panels). This feedback loop continued such that sprat evidently were able to break out of their *predator pit* constraint (Fig. 6d, left panel) and take over dominance of the system. Meanwhile the *larval predator pit* for cod had deepened, and their production rate (reproductive success) had fallen, moving the intersection point (circled in Fig. 6d, right panel) to the right of that diagram, even as the continued overfishing of cod pushed the cod abundance level to the left. Evidently, the abundance level finally intersected the critical intersection point, and the cod "fell into the pit". Thus, even when hydrographic conditions conducive for survival of early life stages of cod were restored due to bottom water renewal that occurred as a result of a major inflow of highly saline water associated with strong westerly gales that occurred in January, 1993 (Matthäus and Lass, 1995), recruitment of cod remained "locked in" to far below average levels (Köster and Möllmann, 2000). The *wasp-waist* species have continued to maintain their dominance of the system, evidently by continuing to impose a *larval predator pit* for cod eggs and larvae that is sufficiently deep to prevent the cod from building a sufficient abundance level to begin to pare down the clupeid populations so as to again re-impose its own dominance over the trophic system (i.e., to reverse the direction of feedback loop operation so as to effect a breakout of its *larval predator pit* and to drive the clupeids back down to their levels of three decades ago).

9. Summary and concluding comments

The small, pelagic, planktivorous fishes that operate at the *wasp-waist* levels of many important marine ecosystems do not act merely as passive conduits of trophic perturbations that may originate at the lowest ("bottom up") or highest ("top down") trophic levels. Rather they possess key attributes that appear to afford them particular power to directly originate, based on their own internal dynamics, powerful trophic transients that can travel both upwards and downwards through the ecosystem, thereby imposing major effects on the trophic levels both above and below.

These key attributes of the *wasp-waist* populations include the following:

1. They have complex life histories coupled with short life cycles. This combination tends to produce large population variations.
2. One single-species population often may represent the preponderance of the biomass existing its trophic level. Consequently its variations in abundance will tend to propagate to both higher trophic levels (which may depend on it as a major food item) and to lower trophic levels (on which it may exert very heavy grazing pressures).
3. They represent the lowest trophic level that is mobile and are consequently capable of relocating their area of operation according to their own internal dynamics. Major changes in their distribution tend to reorganize the spatial pattern of trophic interactions in the ecosystem.
4. They may prey heavily upon the early life stages of their predators, thereby forming an unstable feedback loop in the trophic system. The resulting instability in the trophic system may precipitate abrupt and radical "regime shifts" (Bakun, 2005a).

There have been a number of events in which *wasp-waist* populations have fallen to extremely low biomass, while evading outright extinction, or have suddenly explosively increased from such low biomass levels. This suggests a "*predator pit*" type of dynamics, offering a refuge from predation when abundance is very low. Between an abundance sufficient to attract interest from predators and an abundance sufficient to satiate available predators, very destructive predation may continually drive the population abundance back down to its refuge level. But if the population abundance somehow increases beyond the satiation point of its local predators, specific predation mortality decreases steadily as the population grows, favoring exponential population increase ("breakout"). This *predator pit* concept appears to offer substantial explanatory power for a number of otherwise puzzling events (Bakun, 1996, 2005a) in the population dynamics of large exploited fish populations. (However, it should be noted that the existence of a low-abundance refuge from natural predators does not imply that an overbuilt industrial fishery, that is freed from energy and oxygen constraints by its access to fossil fuels and thus is immune from the factors producing the natural refuge, could not nullify the refuge and cause outright irreversible extinction).

It is worth emphasizing that in a real regional marine ecosystem, the predator pit topography is undoubtedly highly variable over a range of time and space scales. The production functions are also likely to exhibit a substantial degree of time–space variability. Thus the extension of the functional curves over a range of abundance values (along the *x*-axis in the conceptual diagrams presented in this paper, Figs. 2–6, A.1) is a somewhat artificial construct, intended to impart a diagrammatic (intuitive) notion of how the dynamics represented might be expected to unfold. At any real point in actual time and space, there are only two points on such a diagram that have tangible reality. These are the intersections of a vertical line representing the current abundance level (on the *x*-axis) with the predator pit and production rate functions respectively. Whenever the production rate exceeds the predation mortality rate, the abundance will be growing, instantaneously at least, in an exponential manner (i.e., diagrammatically, the *x*-value that corresponds to current prey abundance is in such a case positioned to the right of the theoretical "critical intersection point" that is circled in Fig. 4). When the mortality rate exceeds the production rate, the abundance declines (falls toward the "pit"). It is the variability of these topographies in time and space that permits breakouts to occur, and also (recalling the discussion in Section 5) determine the success of that incipient breakout in fomenting a cascading expansion of the stock to larger and larger space scales, so as to establish a durable shift to a higher abundance level for the fish stock as a whole.

Several examples of application of the *predator pit* concept to clarify otherwise puzzling aspects of marine population ecology have been presented. It was suggested in Section 5 that a "first order" explanation for the observed patterns of progressive geographical habitat expansion as abundance of a *wasp-waist* population increases might lie in the export of excess individuals, from locations where a breakout has already occurred, to help "fill up" the *predator pits* in new areas to prime additional breakouts of biomass that can then be exported to additional new areas. In Section 7, the effects of El Niño-type shifts in the background system productivity level on the interactions of *larval predator pit* depths with larval production and growth rates were offered as a rationalization of the out-of-phase alternations of abundances of anchovies and sardines in many regional

systems that evidently occur without substantial direct adverse interactions between the two species groups. In Section 8, the interaction of environmental processes and fishery exploitation was interpreted as causing a regime shift in the Baltic Sea, wherein the dominant predator population (cod) collapsed in concert with establishment of dominance of that ecosystem by the *wasp-waist* clupeid populations (herring and sprat), the cod's natural prey. In this case, the *predator pit* for the clupeids was shallowed by declining cod abundance, and the *larval predator pit* for cod was deepened as a result of resulting increases in clupeid abundance. Continued overfishing (that might perhaps have not constituted overfishing in more normal circumstances) evidently pushed the cod abundance toward the critical intersection point in its *larval predator pit* diagram, such that the cod finally "fell into the pit" and durable dominance of the system by the clupeids was established.

Evidently that in some situations, juveniles of particularly abundant demersal or semi-demersal fish populations may from time to time form an effective *wasp-waist* for a marine ecosystem. This may occur when a particular opportunity (e.g., when a population collapse of a dominant *wasp-waist* component that may at other times impose a controlling *larval predator pit*) provides the basis for a population "breakout" (see, for example, the discussion in Section 3 of the triggerfish explosion off tropical west Africa that coincided with a collapse of the *Sardinella aurita* fishery off Ghana).

Acknowledgements

Appendix A. Derivation of a functional form for the "predator pit"

Variables

Let x denote the density of the prey population (either numbers or biomass, per unit of habitat space).

Let p denote the corresponding density of the predator population.

Let k denote the effective *fractional encounter rate*, i.e., the typical fraction of a unit of habitat space that is effectively searched or filtered per unit time by a unit density of the predator population. (In the special case of interaction of a moving prey species with a relatively stationary "ambush" predator species, k would denote the fraction of the prey population typically encountering a unit density of the predator population per unit time.)

Let e denote the capture efficiency of the predator (for a predator that is so efficient that it would inevitably capture every prey it encounters, e would equal 1; in nearly all real cases e must be significantly less than 1).

Let x_0 denote the prey density that represents the "threshold of interest" to the predator (at prey densities below x_0, the predator does not attempt to locate or capture this category of prey).

Let x_S denote the *satiation prey density*, i.e., the prey density above which further increases in prey density yield no resulting increases in the rate of consumption (because the predators are already consuming the maximum amount per unit time that they are capable of processing).

Let M represent the *fractional mortality rate* of the prey species due to predation by the predator species (i.e., the fraction of prey consumed in a unit of habitat space per unit time).

Functional relationships

For $x < x_0$, (i.e., below the *threshold of interest*) there is no prey mortality:

$$M = 0 \tag{A.1}$$

For $x_0 \leqslant x \leqslant x_S$, the predators remove all they can capture (i.e., $k \times p \times e \times x$), and so the *fractional mortality rate* is

$$M = (k \times p \times e \times x)/x = k \times p \times e \tag{A.2}$$
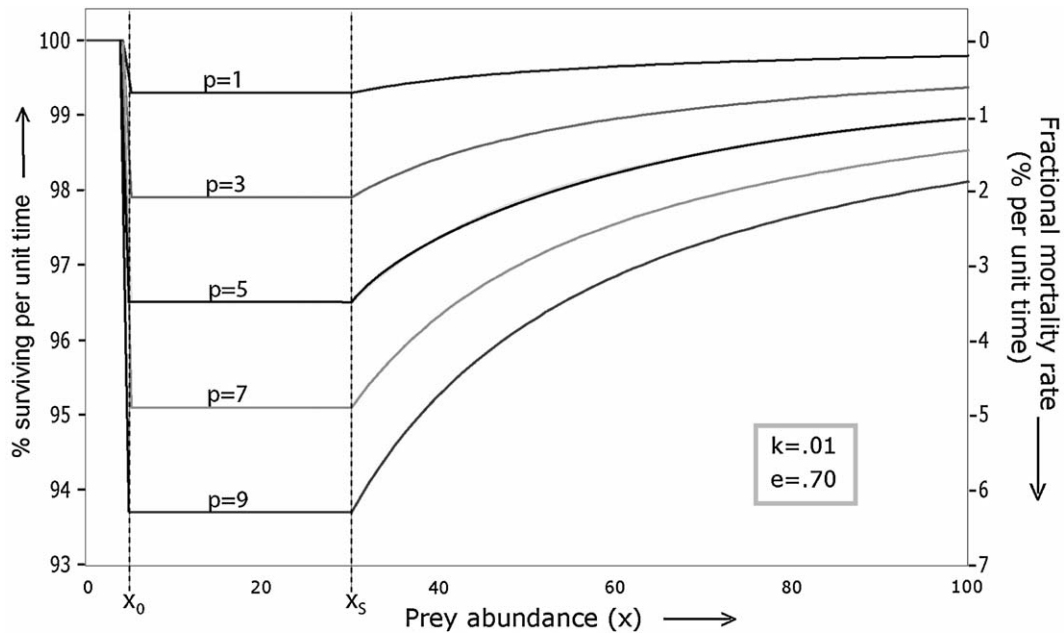
Fig. A.1. An example computation of a *predator pit* function (Eqs. (A.1)–(A.4)) for several different values of predator density, *p*, based on the following arbitrary parameter choices: $k = 0.01$, $e = 0.7$, $x_0 = 5$, $x_S = 30$ (see Appendix A).

For $x > x_S$, predators are unable to increase their rate of consumption above that attained at the "satiation" prey abundance level, x_S, and so

$$M = (k \times p \times e \times x_S)/x \tag{A.3}$$

(Note that the maximum prey density, x_{max}, that a unit predator density can possibly consume per unit time is thus given by $x_{max} = k \times e \times x_S$).

The *survival rate* (percentage of prey surviving per unit time in a given unit of habitat space) is given by

$$S = 1 - M \tag{A.4}$$

Example *predator pit* functions, computed according to (Eqs. (A.1)–(A.4) are illustrated in Fig. A.1. Note that the fractional mortality and survival rates have been converted to percentages (i.e., the computed fractional rates multiplied by 100%) in the labeling of the axes of the various figures presented in this paper.

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